Déterminants multi-échelles des assemblages d'arthropodes et de plantes en plaine inondable. L'exemple de la Vallée de la Loire

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Résumé

Les assemblages d'espèces sont contraints par de nombreux facteurs biotiques et abiotiques s'exerçant aux échelles locales et paysagères. En plaine alluviale, ils sont de plus exposés à des perturbations liées aux crues et à la gestion des milieux. Ces deux facteurs sont particulièrement importants au sein des prairies inondables de la vallée de la Loire qui sont le plus souvent gérées par la fauche (mais aussi par le pâturage) et hébergent des espèces animales et végétales considérées comme patrimoniales et sensibles à la gestion et à l'inondation.

Les déterminants des assemblages d'arthropodes (araignées et carabiques) et de plantes ont été étudiés sur la Vallée de la Loire et les Basses Vallées Angevines lors de trois campagnes de terrain entre 2011 et 2013. Concernant les arthropodes épigés, nous avons pu démontrer qu'à l'échelle locale, la biomasse végétale est un facteur déterminant de la diversité de carabiques soulignant un contrôle « bottom-up » de cette dernière. Ce groupe apparaît en outre être plus sensible que les araignées à l'effet des crues de printemps (ces deux groupes restant les moins sensibles parmi les arthropodes). L'effet des inondations reste cependant dépendant de la configuration paysagère locale et notamment de la présence de haies.

La gestion des prairies par la fauche est depuis longtemps reconnue comme ayant un impact fort, le plus souvent négatif, sur les communautés d'arthropodes. Cette étude a démontré que les effets des retards de fauches mis en place pour la conservation de l'avifaune se font sentir uniquement à court terme : ils se révèlent négatifs pour les carabiques de grande taille alors que les fauches précoces le sont pour les araignées.

La connaissance des habitats est essentielle à la compréhension des facteurs influençant les communautés à large échelle. Dans les plaines inondables, les facteurs régissant les assemblages d'espèces végétales sont l'humidité (liée au régime de crue) et la gestion. Dans cette étude, nous avons défini les types d'habitats prairiaux présents en Vallée de la Loire et démontré la pertinence du couplage d'une approche phytosociologique et de la télédétection pour la cartographie large échelle des habitats.

Si les impacts de la gestion et des crues ont été démontrés individuellement, leur importance relative reste peu connue. Il apparaît que les perturbations stochastiques telles que les crues constituent des déterminants de la diversité et de la densité d'arthropodes et de végétation bien plus importants que la gestion. Cependant, la part relative des facteurs locaux et paysagers (occupation du sol et configuration) dans les variations de diversités (α et β) varie fortement selon les groupes et la composante de diversité étudiée.

Notre travail constitue une première en termes de linéaire de bassin versant couvert dans le cadre d'une étude portant sur les assemblages d'arthropodes. Si elle confirme l'importance de certains facteurs aux échelles locales et paysagères, notre étude démontre en outre l'importance centrale

de l'humidité et donc des crues dans la structuration des assemblages ainsi que le rôle majeur du paysage. Enfin, notre travail souligne la nécessité d'une approche large échelle dans la gestion des milieux prairiaux en zone inondable.

Abstract

Species assemlblages are stuctured by biotic and abiotic factors acting at local and landscape scales. In floodplains, assemblages are also exposed to perturbations, mainly due to flooding and management. These perturbations, are particularly important in the meadows of the Loire Valley which are managed by cutting and grazing and host rare animal and plant species sensitive to management and flooding.

The main factors structuring arthropod (spiders and carabids) and plant assemblages were studied in the Loire Valley during three field campains between 2011 and 2013. Regarding arthropods, we demonstrated that plant biomass is an important driver of local carabid species richness and density. This underlines the existence of a "bottom-up" control of carabid diversity. Besides, carabids seem more sensitive than spiders to spring floods, spiders and carabids being considerabely less impacted than other arthropods. We also found recolonisation process to be dependant of the landscape configuration, mainly the hedges that act as a refuge.

Meadow management by cutting has long been recognized to have a huge, mostly negative, impact on arthropods assemblages. Our study demonstrated that delaying cutting date for birds conservation, has only short term impact : large carabids are negatively affected by late cutting and spiders by early cutting.

A better knowledge of habitat spatial repartition is essential to improve the understanding of factors structuring assemblages at large scale. In flooded meadows, the main factors are wetness (linked to flooding) and management. In our study, we defined habitat types presents in the Loire Valley. Besides, we successfully mapped those habitats coupling a phytosociological approach and remote sensing techniques.

Whereas we demonstrated the importance of flooding and management, their relative importance remains poorly known. We found stochastic perturbations, such as flooding, being a more important driver of arthropod and vegetation diversity and density than management. Nevertheless, the relative contribution of local and landscape (composition and structure) factors in α and β diversities varied greatly with groups and diversity component under study.

Our work is unique, by its amplitude along a major river catchment regarding arthropods. Unless our study confirmed the importance of some classical drivers at local and large scale, it also demonstrated that wetness, and so flooding, are the main drivers of assemblages. The major importance of landscape against local factors on arthropods was also confirmed, including for spiders. Finally, our work underlines the need of large scale approach in management and conservation planning of biodiversity in flooded meadows.

Table des matières

Introduction générale

Le perte généralisée de biodiversité est devenue une préoccupation majeure au niveau mondial depuis la signature de la convention de Rio en 1992 et a donné lieu a un fort développement de la recherche en biologie de la conservation (Spray et al., 2004). En Europe, la politique de conservation de la nature est principalement basée sur deux directives visant à conserver des listes d'espèces et d'habitats dits prioritaires à l'échelle Européenne: la Directive Oiseaux (79/409/EEC) et la directive Habitats Faune Flore (92/43/EEC).

Dans ce cadre, le monde de la recherche est de plus en plus sollicité par les gestionnaires d'espaces naturels et les autorités afin de disposer d'outils permettant de comprendre, d'évaluer et de prédire la répartition de ces espèces et habitats rares (Negro et al., 2013). Cependant, les politiques de gestion basées sur la conservation d'une ou d'un petit nombre d'espèces supposés être des espèces dites "parapluie" ou encore d'habitats rares, peut se révéler contre-productive et mettre la biodiversité locale en danger (Lambeck, 1997). La mise en place de mesures favorisant la richesse spécifique végétale en prairie a par exemple aboutie à la disparition d'une espèce rare de papillon (*Colias myrmidone*) en République Tchèque (Konvicka et al., 2007). Les exemples de ce type sont nombreux et ne concernent pas uniquement les invertébrés mais aussi les plantes (Severns, & Moldenke, 2010) et les mammifères (Berger, 1997).

Les principes de la biologie de la conservation s'orientent désormais logiquement vers la conservation des assemblages d'espèces. En effet, ce sont ces assemblages qui définissent la richesse et la composition fonctionnelle des communautés; ces deux composantes semblant être des déterminants essentiels des fonctions et services joués par les écosystèmes (Díaz, & Cabido, 2001; Petchey et al., 2004). Ceci est d'autant plus vrai dans un contexte de changement climatique global responsable de perturbations induisant à moyen terme de profonds changements dans les écosystèmes.

Afin d'anticiper la réponse des écosystèmes et plus particulièrement des assemblages d'espèces à ces perturbations, il est essentiel de mieux en comprendre la structuration: quels sont les facteurs les plus prégnants et à quelle(s) échelle(s) s'exercent-ils?

Les politiques de conservation ignorent largement certains groupes. Ainsi, alors qu'ils représentent l'essentiel de la diversité (80% des espèces décrites) et de la biomasse des écosystèmes, les arthropodes épigés ne font pratiquement pas l'objet de mesures de protection (Cardoso et al., 2011). A titre d'exemple, la Directive Habitats Faune Flore ne comprend, en Annexe II, que 26 espèces d'insectes sur les dizaines de milliers présentes en France contre 166 des 545 espèces d'oiseaux présentes. Notre travail portera donc principalement sur les arthropodes, en tant que composante majeure de la biodiversité mais aussi en raison de leur importance fonctionnelle dans l'écosystème.

Dans les milieux naturels, les assemblages d'espèces sont structurés par des facteurs biotiques (interactions entre espèces: compétition, prédation, symbiose...) et abiotiques (physico-chimie du milieu) (Hunter, & Price, 1992). Une large part des études considère que les communautés sont principalement structurées par des facteurs biotiques (Dunson, & Travis, 1991), plus particulièrement les interactions entre espèces et ignorent que la plupart des communautés s'expriment au sein de gradients de température, d'humidité et de chimie du sol (McGill et al., 2006). Ces facteurs abiotiques peuvent par ailleurs conditionner la nature des interactions entre espèces (Dunson, & Travis, 1991; Meester et al., 2011) et doivent donc être pris en compte dans la définition de la niche écologique des espèces.

Les perturbations peuvent elles aussi être un des facteurs majeurs influant sur les communautés. Elles sont en effet une source importante d'hétérogénéité spatiale et temporelle dans la structure de ces dernières ainsi qu'un filtre de sélection naturelle (Sousa, 1984). Elles sont le plus souvent associées aux facteurs abiotiques (crues, feu...) mais peuvent aussi être biotiques (prédation, pâturage, modifications du substrat...) et affectent les communautés (depuis l'individu jusqu'à l'écosystème) et le paysage de façon différente (Rykiel, 1985).

Enfin, la structuration des communautés est aussi le résultat d'interactions complexes entre facteurs s'exerçant à l'échelle locale et à large échelle. L'importance relative des facteurs abiotiques et biotiques varie avec l'échelle considérée, les deux types interagissant à l'échelle locale alors que les facteurs abiotiques et notamment environnementaux sont plus prégnants à large échelle (Menge, & Olson, 1990).

A l'échelle locale, les communautés sont appréhendées en termes d'abondance, de composition, de richesse spécifique (diversité α) et de diversité fonctionnelle. L'étude des communautés à plus large échelle introduit en outre la notion de diversité β. Cette dernière correspond aux changements de compositions spécifiques entre lieux (McKnight et al., 2007) et se décompose en taux de remplacement des espèces et différence de richesse entre sites (Baselga, 2010).

Ce sont donc les déterminants de la structuration des assemblages d'espèces en terme d'abondance, de diversité (α et β) et de traits fonctionnels que nous nous efforcerons d'étudier dans ce travail et cela à aux échelles locales et paysagères ainsi qu'à différents pas de temps.

La présente étude se situe dans les plaines inondables de la Vallée de la Loire, des Basses Vallées Angevines et de la Vienne (France). Les plaines inondables sont considérées comme l'un des habitats les plus riches et productifs dans les régions tempérées (Gerken, 1988). En effet, situées en bordure des grands fleuves présentant des fonctionnements hydrologiques naturels (The Royal Society for the Protection of Birds, 1997), ces plaines présentent une grande diversité d'habitats. De plus, les perturbations liées à l'alternance d'inondations et de phases de sécheresse sélectionnent des espèces animales et végétales adaptées à ces conditions particulières (Marx et al., 2012). Les stratégies d'adaptation des invertébrés à ces conditions ont été largement étudiées dans des milieux où les inondations sont prévisibles tels que le bassin de l'Amazone (Adis, & Junk, 2002) ou dans

le Pantanal (Wantzen et al., 2011). Les études portant sur des milieux où des inondations plus aléatoires (printanières ou estivales) peuvent intervenir en plus des inondations hivernales sont beaucoup plus rares, en dépit d'un récent regain d'intérêt (Rothenbücher, 2004; Gerisch et al., 2011; Gerisch et al., 2012; Gerisch, 2014).
En Europe, les grands fleuves ont fait l'objet de nombreux aménagements visant à lutter contre ces inondations (barrages, drainages, levées...) (Dankers, & Feyen, 2008). Ces aménagements ont perturbé durablement le fonctionnement écologique de ces écosystèmes. En limitant la fréquence des crues, ils ont aussi permis l'installation d'activités agricoles et ont débouché, dans certains cas, sur une urbanisation et une industrialisation importantes de ces zones. Les plaines inondables figurent donc parmi les habitats naturels les plus en danger au niveau mondial (Tockner, & Stanford, 2002).
Au bords des grands fleuves présentant encore un fonctionnement hydrologique peu perturbé les activités agricoles sont cependant restreintes et essentiellement liées aux prairies pour la production de foin et l'élevage. Ainsi, les prairies semi-naturelles peuvent représenter jusqu'à 45% de l'occupation du sol (c'est le cas en Vallée de la Loire: Vaudelet, 2008).

Au sein des agro-écosystèmes, les prairies permanentes sont généralement considérées comme les habitats les plus riches en espèces (Noordijk et al., 2010; Woodcock et al., 2011). Elles sont de plus une source reconnue de diversité pour les cultures (Benton et al., 2003; Purtauf et al., 2005) notamment concernant les arthropodes épigés. Cependant, les arthropodes associés aux prairies semi-naturelles sont particulièrement menacés en Europe (e.g. Thomas et al., 1994; Duelli, & Obrist, 2003), qu'il s'agisse des espèces spécialistes ou généralistes (Cizek et al., 2012). En effet, suite l'intensification des pratiques agricoles (Millennium Ecosystem Assessment, 2005), les prairies constituent un milieu en constante régression. Elles restent néanmoins le mode d'exploitation majoritaire dans les plaines alluviales présentant des fonctionnements hydrologiques préservés.

Parmi les arthropodes, nous nous sommes plus particulièrement intéressés aux araignées et aux coléoptères carabiques. En effet, ces deux groupes sont capables de coloniser presque tous les habitats terrestres (Rothenbücher, 2004), sont particulièrement diversifiés (1725 espèces d'araignées ASFRA, 2013 et 1050 espèces de carabiques Coulon et al., 2012 en France) et sont parmi les arthropodes les plus abondants (Lövei, & Sunderland, 1996; Drapela et al., 2008). Araignées et carabiques présentent de plus des traits fonctionnels variés et complémentaires. Ainsi, alors que les araignées sont exclusivement prédatrices, certaines espèces de carabiques sont polyphages et d'autres phytophages. On distingue en outre chez les araignées des groupes présentant des modes de chasses et des strates de vie différents réagissant donc différemment aux conditions de milieux et notamment à la végétation. Les modes de dispersion sont aussi complémentaires: les araignées dispersent de façon active par course au sol ou passive par ballooning; les carabiques dispersent eux aussi au sol ou par le vol actif en fonction du développement de leur muscles alaires et de leurs ailes

(Desender, 2000). On suppose donc généralement que les carabiques ont de meilleures capacités de dispersion. La taille des individus joue bien sûr sur ces dernières mais aussi sur leur capacité de résistance aux perturbations. Les deux groupes sont considérés comme particulièrement sensibles à ces perturbations et aux conditions de milieu à l'échelle locale mais aussi à large échelle.
Ces conditions de milieu, quelle que soit l'échelle à laquelle on les appréhende, sont soit en grande partie liées à la végétation (structure spatiale de l'habitat, épaisseur de litière, présence de proies), soit intégrées par cette dernière (humidité, nature et niveau trophique du sol...). La végétation constitue donc l'un des facteurs explicatif essentiel à la compréhension de la structuration des assemblages d'espèces d'arthropodes. Ainsi, alors que la plupart des études cherchant à expliquer les liens plantes/arthropodes se concentrent sur des descripteurs tels que la diversité spécifique ou fonctionnelle, l'une des rares études a avoir pris en compte la composition spécifique de la végétation a montré que cette dernière était le plus important prédicteur de la composition spécifique des communautés d'arthropodes (Schaffers et al., 2008). Nous avons donc choisi d'intégrer ce compartiment biologique non seulement en tant que variable explicative à l'échelle locale mais aussi d'en étudier les déterminants à large échelle. On se place ainsi dans le cadre de l'écologie des communautés qui étudie les interactions entre les organismes vivant dans une aire donnée. Ce travail se place ainsi dans le cadre d'un projet plus large visant à étudier le "Fonctionnement écologique des ensembles prairiaux de la Vallée de la Loire" et qui intègre à ce titre un volet avifaune prairiale.

Les facteurs abiotiques les plus fréquemment cités comme régissant les communautés des milieux prairiaux, sont l'humidité (Blake et al., 2003; Desender, & Maelfait, 1999; Pétillon et al., 2010) ayant un rôle sur la composition spécifique des assemblages et la richesse en azote du sol influant négativement sur la richesse spécifique (Grace, 1999; Plantureux et al., 2005). Les prairies sont de plus généralement maintenues ouvertes par deux modes de gestion, l'un ponctuel et l'autre continu, qui peuvent être combinés: la fauche et le pâturage. Ces deux perturbations du milieu permettent d'empêcher la fermeture par embroussaillement (Grime, 2001). Le mode de gestion présente une importance cruciale dans la structuration des réseaux trophiques. En pâture, les mega-herbivores contrôlent la ressource, qui contrôle les micro-herbivores et par cascade, leurs prédateurs. Dans les prairies de fauche, en l'absence de mega-herbivores, les interactions biotiques sont de type top-down (contrôle par les prédateurs) et/ou bottom-up (contrôle par la ressource) (Rzanny et al., 2012). L'existence d'un contrôle de type bottom-up a déjà été démontrée dans les grandes prairies américaines gérées par la fauche (Patrick et al., 2008). **Nous avons cherché, dans un premier temps (Chapitre 1), à tester l'existence, à l'échelle locale, de ce type de contrôle dans des prairies de fauche soumises à une source de perturbation supplémentaire: les crues**. En effet, nous avons supposé que la forte productivité des prairies humides (liée aux apports de matière organique par les crues) entraînerait une prévalence du contrôle de type bottom-up.

L'impact de la fauche sur la diversité faunistique est généralement considéré comme négatif et plus particulièrement sur les arthropodes (Ausden, 2007) dont les araignées (Bell et al., 2001) ou les cicadelles (Rothenbücher, & Schaefer, 2006). La fauche est un événement de type catastrophique (Morris, 2000), entraînant la destruction directe des individus et un changement drastique des conditions de milieux (humidité, température, structure de végétation) (Bell et al., 2001). Elle affecte négativement l'abondance et la diversité spécifique et fonctionnelle des communautés. Les carabiques semblent être moins sensibles à la fauche (Mayr et al., 2007), l'effet de cette dernière se faisant surtout sentir sur l'abondance relative des espèces (Haysom et al., 2004).
L'impact négatif de la fauche sur la survie des oiseaux prairiaux a été largement démontré (Britschgi et al., 2006) et a justifié la mise en place de retards de fauche dans la plupart des pays d'Europe à travers les mesures agri-environnementales (MAE). L'efficacité de ce retard sur la survie des juvéniles d'oiseaux prairiaux est souvent considéré comme indiscutable (Brereton et al., 2007) mais a récemment été remise en cause dans des contextes de milieux perturbés par les crues (Besnard et al., 2014). Son impact sur les arthropodes a été très peu étudié en milieu prairial. **Nous avons donc testé dans un second temps (Chapitre 2), l'impact de la date de fauche (et par extension des MAE) sur les communautés d'arthropodes dans des contextes d'habitats soumis aux perturbations liées aux crues**. Étant donné que le décalage des dates de fauches a un impact reconnu sur la diversité végétale (Critchley et al., 2007), les fauches précoces favorisant les espèces pérennes et compétitives, on suppose l'existence d'un effet à long terme de la date de fauche, notamment sur les araignées. Ce groupe est en effet reconnu comme sensible à la structure de végétation (Dennis et al., 1998). Des effets sont attendus principalement en termes fonctionnels, les araignées à toile étant les plus touchées. A court terme, nous attendons des effets négatifs sur l'abondance et la richesse liées à la phénologie des groupes: les effets de la fauche devraient être plus importants lorsque l'activité est maximale.

Les crues constituent une autre source importante de perturbation des écosystèmes prairiaux. L'importance de ces dernières dans la structuration des communautés a fait l'objet de nombreuses investigations concernant aussi bien la flore (par exemple Follner, & Henle, 2006; Violle et al., 2007), que la faune (par exemple Marmonier et al., 1992; Lambeets, 2009). Contrairement à ce qui a été observé dans les systèmes où la régularité des crues permet la sélection de traits adaptatifs (Adis, & Junk, 2002), en Europe les crues sélectionnent particulièrement des espèces animales ubiquistes à fort potentiel de dispersion et de reproduction, recolonisant les milieux après crue (Zulka, 1994). Le régime d'inondation agit en revanche sur les plantes comme un filtre sélectionnant les traits les plus adaptés à la résistance à la crue (Ilg et al., 2008; Violle et al., 2007). Si les stratégies adoptées par les différents groupes d'arthropodes sont bien connues, très peu d'études ont comparé les capacités de recolonisation des différentes familles d'arthropodes à court terme. Par ailleurs, bien que de nombreuses études aient comparé l'impact à long terme des inondations sur les araignées et les carabiques, peu ont réalisé ces comparaisons quant à l'impact à court terme. L'importance de la

présence de refuges (émigration verticale) dans l'évitement des crues a de plus été mis en évidence (Adis, & Junk, 2002) ainsi que le rôle non négligeable du paysage dans la survie des arthropodes (Ballinger et al., 2007). **Nous avons donc choisi d'étudier les processus de recolonisation des prairies par les arthropodes après retrait des eaux et d'évaluer l'importance du paysage dans ces processus (Chapitre 3)**. Nous attendons ici une recolonisation rapide par des espèces généralistes ayant de fortes capacités de dispersion (Linyphiidae et petits carabiques ailés) ou par des espèces capables de résister / éviter la submersion. Les prairies non inondées, les boisements et les haies sont supposés jouer le rôle de refuges.

Les assemblages de plantes sont eux aussi largement influencés par l'humidité du sol et le mode de gestion, notamment dans les milieux prairiaux des grandes vallées alluviales (Foucault, 1984; Bonis et al., 2010). La classification des assemblages d'espèces végétales (ou phytosociologie) est une méthode développé par Braun-Blanquet (1928) connaissant un regain d'intérêt depuis les années 1990, notamment grâce à la politique européenne Natura 2000 se basant sur cette méthode pour définir les habitats à conserver prioritairement. La connaissance de la répartition de ces habitats est essentielle à la compréhension des déterminants de la structuration large échelle des communautés animales. Elle est cependant très coûteuse et ne peut être réalisée dans les milieux les moins accessibles lorsqu'il s'agit d'utiliser les méthodes traditionnelles de cartographie (Zak, & Cabido, 2002). L'utilisation d'images satellites, dont le coût d'acquisition ne cesse de baisser et la résolution d'augmenter, est donc très prometteuse pour la réalisation de cartographies à grande échelle (Mayr et al., 2007). **En nous appuyant sur les travaux de Zak, & Cabido (2002) et Fanelli et al. (2005), nous faisons l'hypothèse qu'il est possible de cartographier les principales associations phytosociologiques ainsi que leurs variantes sur un territoire donné en croisant une approche phytosociologique et la classification supervisée d'images haute résolution**. Ceci permettrait de disposer à large échelle d'une couche environnementale essentielle à la compréhension de la répartition de la faune ainsi que de "proxy" de l'humidité et de la teneur en azote notamment à travers le calcul d'indices basés sur le préférendum des espèces (Ellenberg et al., 1992).

Comme nous l'avons vu, les interactions biotiques et abiotiques structurant les communautés s'exercent à des échelles locales mais aussi à large échelle. Il nous est donc paru important de confronter les résultats acquis à l'échelle locale à une analyse à plus large échelle. Le fait de réaliser des échantillonnages à large échelle permet en outre d'intégrer aux analyses des facteurs paysagers aux analyses et d'augmenter la portée des résultats en terme de généralisation.
Les mesures agri-environnementales, abordées précédemment, représentent un investissement plus que conséquent au niveau Européen avec un total de 34,9 millions d'euros investis sur l'exercice 2007-2013 (COM, 2008). Leur efficacité a été démontrée à plusieurs reprises (Brereton et al., 2007; Albrecht et al., 2007) mais dans certains cas, elles se sont aussi révélées inopérantes sur

la flore et les oiseaux (Kleijn et al., 2001) et même négatives sur les papillons (Konvicka et al., 2007). Sachant que les perturbations constituent l'un des principaux facteurs structurant les communautés d'arthropodes, **nous avons souhaité évaluer, dans le chapitre 5, le rôle joué par les mesures préconisées par les MAE (retard de fauche et limitation des intrants azotés) sur les diversités d'arthropodes et de plantes à large échelle dans un contexte de perturbations par les crues**. L'impact des améliorations de gestion étant parfois négligeable par rapport à celui de facteurs tels que le paysage (Schmidt et al., 2005), nous supposons ici que l'impact positif généralement constaté sur la flore et les arthropodes ne sera pas décelable, les effets des crues étant bien supérieurs.

A large échelle, carabiques, araignées et plantes sont influencés par le paysage: par sa composition (l'occupation du sol) mais aussi par son organisation spatiale (sa connectivité) (araignées: Benton et al., 2003; Purtauf et al., 2005; Hendrickx et al., 2007; carabiques: Duflot et al., 2014; Al Hassan, 2012; Burel, 1989; végétation: Lundholm, 2009). L'importance des variables paysagères pour les araignées est cependant encore discutée et pourrait dépendre de l'habitat étudié (Jeanneret et al., 2003). En lien avec le développement de la recherche des déterminants de la diversité β, de récents efforts sont en cours afin d'évaluer l'importance relative des facteurs locaux, paysagers mais aussi spatiaux dans la structuration des assemblages d'espèces à large échelle. Les résultats semblent encore une fois différer selon les groupes étudiés, les milieux et la composante de biodiversité que l'on souhaite expliquer. Par exemple Blanchet et al. (2012) ont montré, qu'en forêt, la diversité α de carabiques est majoritairement influencée par des facteurs locaux. A l'inverse, Boieiro et al. (2013) ont démontré que dans ce même milieu la diversité β est contrôlée par des facteurs spatiaux. En milieu urbain, Braaker et al. (2013) suggèrent que les déterminants de la diversité β dépendent des traits fonctionnels des espèces et notamment de la mobilité : les espèces les plus mobiles répondent à la connectivité du milieu alors que les moins mobiles répondent aux facteurs locaux. Ce dernier point a été mis en évidence chez les araignées par Jiménez-Valverde et al. (2010). **Dans le Chapitre 6, nous avons donc étudié la contribution relative des facteurs locaux et paysagers aux diversités α et β de trois groupes présentant des capacités de dispersion différentes : les araignées, les carabiques et les plantes, cela dans un paysage peu hétérogène mais présentant une connectivité par le bocage très variable**. Une dominance des facteurs locaux sur les diversités floristiques est ici attendue. Pour les araignées et les carabiques, nous attendons une dominance des facteurs paysagers (nature du paysage pour les araignées et connectivité pour les carabiques).

Matériel et méthodes général

Ce chapitre présente de façon générale les sites d'étude et les techniques d'échantillonnage et d'analyses utilisés. Il ne présente donc pas de manière exhaustive l'ensemble des analyses menées, ces dernières étant décrites dans le matériel et méthodes de chaque chapitre.

Présentation du secteur d'étude

Les sites d'études sont majoritairement situés en Pays de la Loire sur la Vallée de la Loire et les Basses Vallées Angevines (BVA) et dans un moindre mesure en Basse vallée de la Vienne (Figures 0.2 et 0.3).

Éléments de géologie

Le secteur d'étude couvre les 300 derniers kilomètres de la Vallée de la Loire entre Saint-Nazaire et Chinon. Sur cette portion, la Loire traverse plusieurs secteurs très différents. Entre Chinon et Angers, la Loire traverse la marge occidentale du Bassin Parisien composée de roches sédimentaires formant notamment en rive gauche une alternance de coteaux et de falaises de tuffeau (Figure 0.1). Sur ce secteur, le lit majeur de la Loire endigué par des levées, est majoritairement constitué de terrains sableux particulièrement sèchants.

A partir d'Angers, la Loire rentre dans le Massif Armoricain et passe donc sur des terrains de type schisteux (schistes jusqu'à Ancenis puis micaschistes jusqu'à Nantes). Les habitats du lit majeur sont, sur cette zone, bien plus hygrophiles et sont dominés par des prairies humides.
Enfin, après Nantes, la Loire entre dans le secteur estuarien dominé par roches sédimentaires (sable) en rive droite et magmatiques (granites) en rive gauche.

Les Basses Vallées Angevines (BVA), sont composées de la Mayenne, du Loir, de la Sarthe et de la Maine. De la confluence de la Maine et de la Loire au nord de l'Île Saint-Aubin, les BVA appartiennent au Massif Armoricain. Tout le secteur nord appartient au Bassin Parisien. Il n'est pas endigué et ne présente que peu de relief. Il constitue en conséquence l'une des zones les plus humides du secteur d'étude.

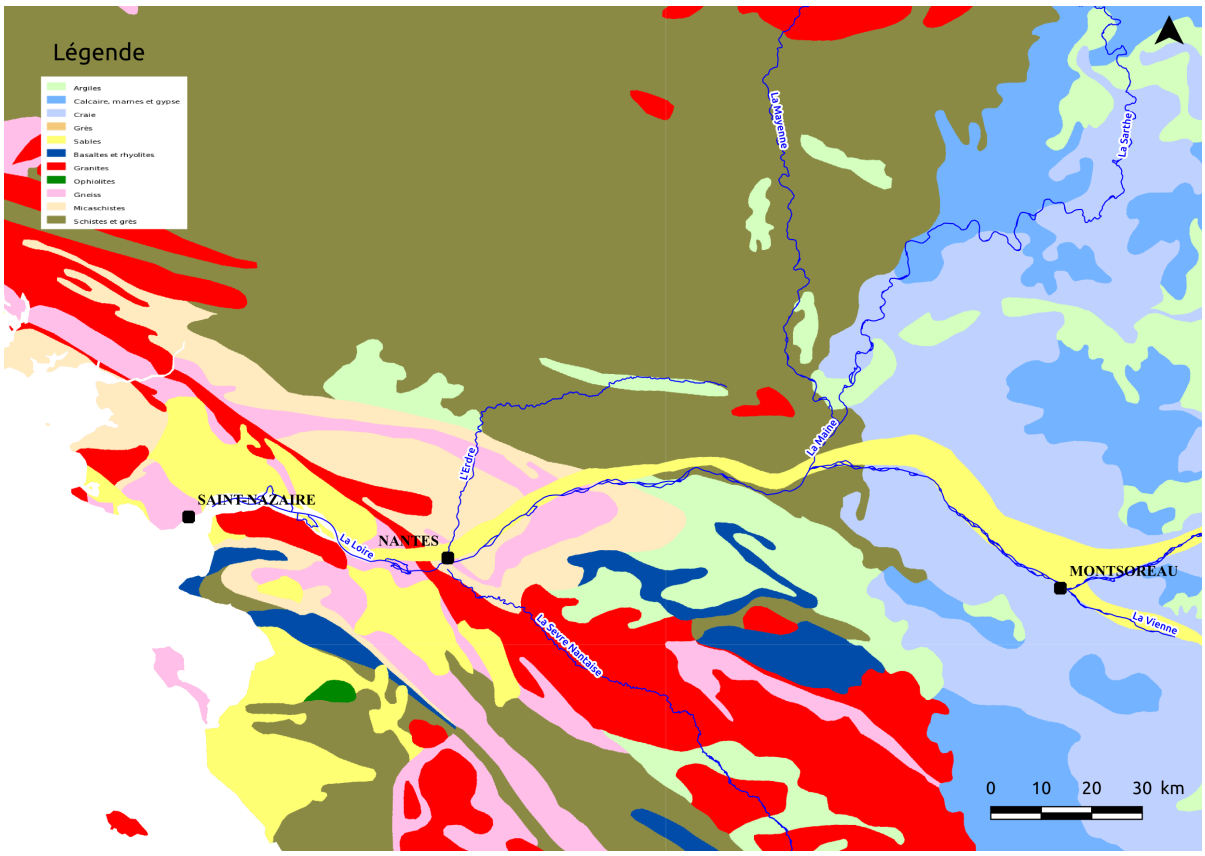

Figure 0.1 – Lithographie simplifiée du secteur d'étude (source: BRGM).

Éléments d'hydrologie

Suite aux aménagements du début du XX$^{\text{ième}}$ siècle (épis et ouvrages sur les bras secondaires), au creusement d'un bassin de marée dans l'estuaire et aux nombreuses extractions de sable, le lit de la Loire présente une forte incision. La ligne d'eau d'étiage s'est ainsi abaissée de 1 à 3 mètres à l'amont de Nantes et de 3,5 mètres à Nantes. Cet abaissement a entraîné un assèchement des zones humides connexes à la Loire, une remontée de front de salinité (jusqu'à Thouaré), le développement d'un bouchon vaseux dans l'estuaire et une augmentation des courants. Ainsi, depuis le début des années 60, sur le secteur d'étude, la Loire présente une hydraulicité moyenne avec des débits moyens journaliers de 914 m^3/s (750 m^3/s sur la période 1965-1985). A Montjean-sur-Loire, le débit peut dépasser les 6000 m^3/s pour les crues remarquables et descendre sous les 100 m^3/s pour les étiages sévères.

La Loire aval subit des crues de type océanique (dues aux longues périodes de pluies souvent hivernales) qui peuvent s'ajouter à des épisodes de type cévenol (fortes pluies sur des périodes courtes). Durant l'hiver, une grande partie du lit majeur est inondée sur une durée allant de un à trois mois. Des crues de printemps (souvent liées à la fonte des neiges) et estivales surviennent à des fréquences plus aléatoires.

Sites d'étude

Les travaux ayant été menés aux échelles locale et large deux type de sites sont à distinguer: les sites ponctuels (Île Saint-Aubin et Marais d'Audibon) et un ensemble de parcelles réparties sur l'ensemble du secteur.

L'Île Saint-Aubin (0 ° 32' 37.7" W, 47 ° 30' 05.6" N) a fait l'objet des études menées à l'échelle locale sur l'arthropofaune (Figure 0.2). Située à l'extrême sud des Basses Vallées Angevines, sur la commune d'Angers, elle est entourée par trois rivières : la Sarthe, la Mayenne et la Maine. L'île est essentiellement couverte de prairies mais comporte aussi quelques peupleraies. D'une surface d'environ 600 ha, elle est majoritairement occupée par des prairies gérées par la fauche et faisant l'objet d'un pâturage de regain. L'île est inondée dans sa plus grande partie pendant un à trois mois durant l'hiver et subit aussi aléatoirement des crues de printemps.

Les marais d'Audubon (1 ° 46' 36.2" W, Lat: 47 ° 14' 07.8" N) ont eux aussi fait l'objet d'une étude à l'échelle locale, cette dernière portant sur la cartographie de végétation (Figure 0.3). Le site est situé en aval de Nantes sur la commune de Saint-Etienne de Montluc, dans l'estuaire de la Loire. Il présente une superficie d'environ 3000 ha, dominée par les prairies de fauches et les pâtures. Il présente une hydrologie particulière liée à sa position estuarienne en bordure du sillon de Bretagne. Il est ainsi soumis à des inondations régulières provoquées par les grandes marées et amenant de l'eau saumâtre. A l'inverse, les zones situées en bordure du sillon de Bretagne sont très humides mais reçoivent les eaux douces du bassin versant.

Pour les études à large échelle, les sites d'échantillonnage sont répartis sur l'ensemble de la zone d'étude incluant la Vallée de la Loire entre Saint Nazaire et Montsoreau, les Basses Vallées Angevines entre Angers et Juvardeil et la Basse Vallée de la Vienne entre Montsoreau et Chinon. Ils ont été choisis afin de couvrir l'ensemble de la gamme de taille de parcelle rencontrée sur le secteur d'étude et de présenter la répartition spatiale la plus homogène possible.

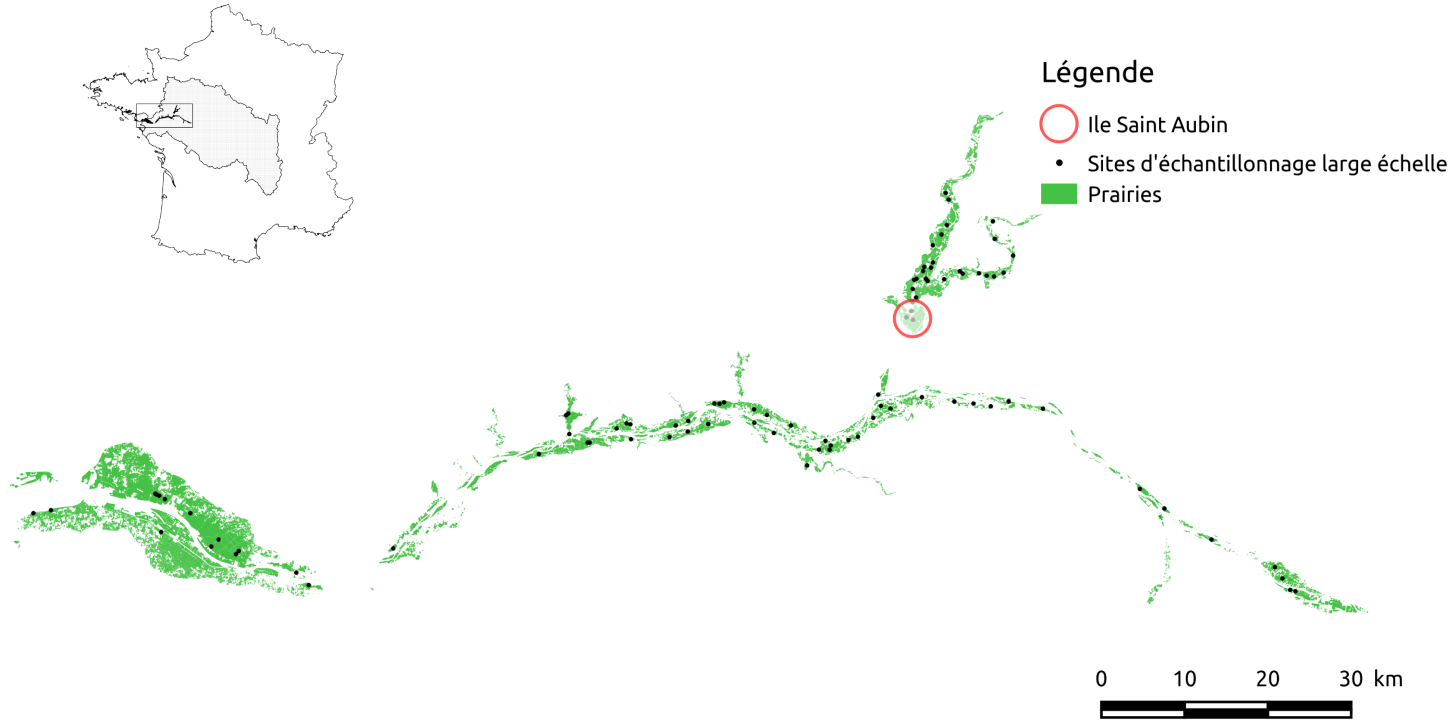

Figure 0.2 – Cartographie des sites d'échantillonnage d'arthropodes entre 2011 et 2013.

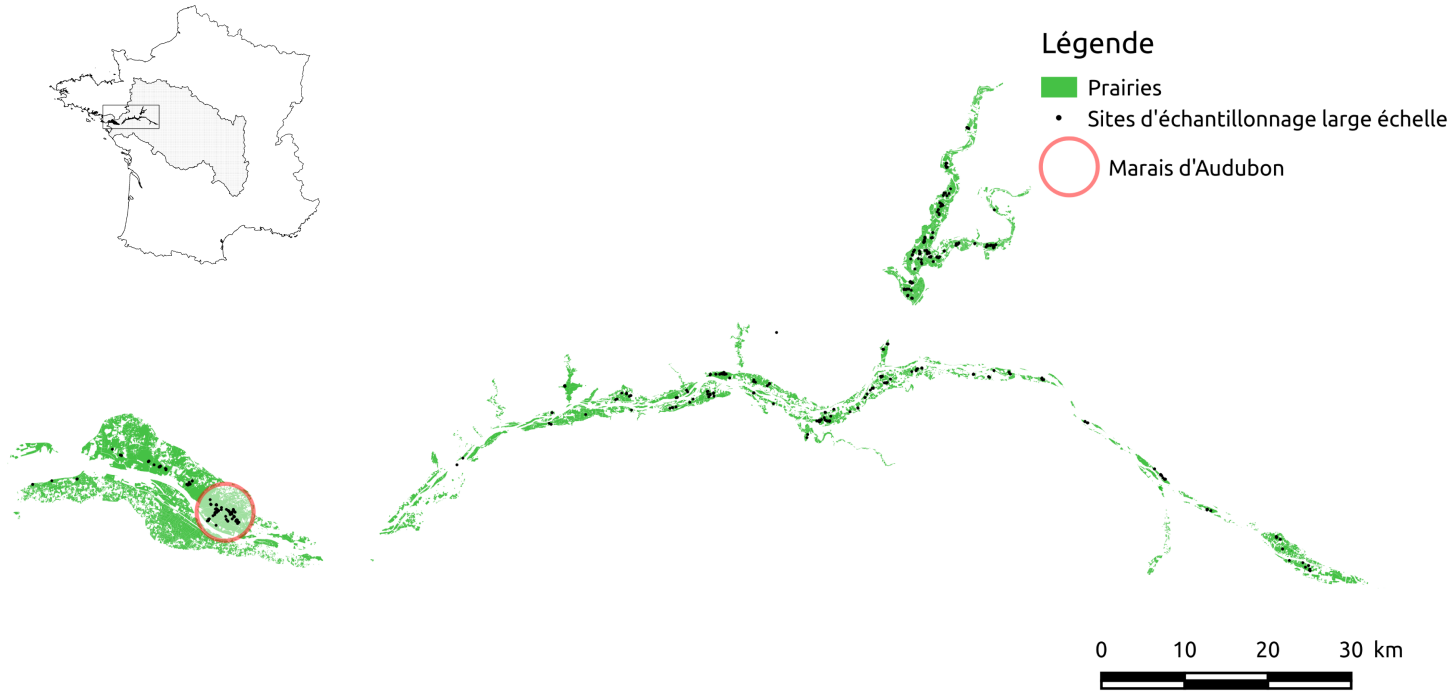

Figure 0.3 – Cartographie des relevés phytosociologiques réalisés entre 2011 et 2013.

Méthodes d'échantillonnage

Arthropodes

Dans cette étude, deux techniques d'échantillonnage des arthropodes terrestres ont été utilisées: le piège d'interception (piège barber) et l'aspirateur thermique (D-VAC). Le piège barber est la technique d'échantillonnage la plus utilisée pour le piégeage des arthropodes épigés (Mommertz et al., 1996) de part son faible coût et sa simplicité de mise en place (Topping, & Sunderland, 1992). Interceptant les individus se déplaçant au sol et plus particulièrement les araignées et coléoptères carabiques (Southwood, 1966), il permet d'obtenir une estimation de l'activité-densité. Piégeant en permanence, il permet d'échantillonner les cortèges d'arthropodes nocturnes et diurnes. L'ensemble de ces avantages nous a amené à sélectionner préférentiellement cette technique et à la mettre en œuvre dès 2011 sur l'île Saint-Aubin.
Cette mise en œuvre est cependant dépendante des conditions de milieux. Ainsi, l'échantillonnage large échelle n'a pu être réalisé en 2011, la sécheresse ayant rendu le sol bien trop dur pour la mise en place des pièges. A l'inverse, la crue de printemps survenue en 2012 a entraîné la perte de 210 des 300 pièges barbers posés sur l'ensemble de la Vallée de la Loire et des Basses Vallées Angevines. Il nous est paru indispensable de mettre en œuvre une technique d'échantillonnage plus rapide (le D-VAC), ne risquant pas d'entraîner la perte du matériel biologique échantillonné et non soumise à l'attente d'un ressuyage complet des 20 premiers centimètres du sol, dans le cadre de notre étude à large échelle. Ce choix s'est révélé judicieux puisqu'une nouvelle crue de printemps a eu lieu en 2013.
L'aspirateur thermique permet d'estimer une densité réelle d'individus et est recommandé lorsqu'il s'agit d'obtenir rapidement un échantillon représentatif des arthropodes épigés (Duffey, 1974). Son efficacité est cependant discutée. Mommertz et al. (1996) considèrent qu'il n'est pas adapté à l'échantillonnage des individus de grande taille (Carabidae et Lycosidae par exemple) ou se terrant dans les anfractuosités du sol (Standen, 2000). A l'inverse, Brook et al. (2008) considèrent qu'avec un effort suffisant, il est adapté à l'échantillonnage de nombreux arthropodes dont les Carabidae.

Les pièges barber sont composés d'un tube PVC de 10 cm de diamètre affleurant le sol et d'un entonnoir permettant d'empêcher les captures accidentelles d'amphibiens et de micro-mammifères. Un pot rempli de conservateur (monoéthylène glycol en 2011 et propylène glycol en 2012) permet de recueillir les individus capturés. L'ensemble du piège est protégé des entrées d'eau par un couvercle (Figure 0.4).

Les pièges sont installés à une distance minimale de 10 m les uns des autres afin de garantir leur indépendance (Topping, & Sunderland, 1992). Afin de limiter l'effet lisière, ils sont aussi installés à une distance minimale de 20 m du bord des parcelles échantillonnées (Topping, & Sunderland, 1992). Les pièges sont vidés tous les 3 à 15 jours selon la fréquence temporelle nécessaire.

Figure 0.4 – Piège barber.

La technique du D-VAC consiste à utiliser un aspirateur thermique (Figure 0.5) permettant d'aspirer l'ensemble des arthropodes présents sur une surface donnée. Il permet donc d'obtenir des densités réelles et n'est pas limité aux espèces errantes. Un aspirateur à feuille (MC CULLOCH GBV 345, Tucson) a été utilisé. Il comporte une bouche d'aspiration de 12,5 cm de diamètre, que l'on place sur le sol afin de réaliser l'échantillonnage. Sur chaque parcelle, 5 séries (i.e. répliquats) d'aspirations sont réalisées. Chaque série consiste en 20 aspirations de 15 secondes chacune (temps nécessaire pour échantillonner l'ensemble des coléoptères carabiques et araignées selon Brook et al., 2008), correspondant à une surface totale de 0,12 m^2. Les échantillons sont immédiatement stockés dans des pots contenant de l'alcool à 70%.

Végétation

Les relevés de végétation ont été réalisés selon la méthode phytosociologique de Braun-Blanquet (1928). Cette technique, particulièrement adaptée à l'étude des assemblages d'espèces (Bouzillé, 2007), répondait particulièrement bien à nos attentes. Nous souhaitions en effet pouvoir intégrer à nos modèles un facteur correspondant au type d'habitat et éventuellement un nombre d'espèces végétales. De plus, elle est utilisée pour la définition des Habitats Natura 2000 et s'inscrit donc parfaitement dans la philosophie de ce travail, principalement orienté sur la biologie de la conservation.

Le relevé phytosociologique se situe dans une unité de végétation homogène. Chaque relevé est réalisé sur une surface de 16 m^2 (4x4 m) comme recommandé par Chytrý, & Otypkova (2003). Sur cette surface, le recouvrement de chaque espèce végétale est exprimé selon l'échelle de Braun-Blanquet. Les relevés ont été géolocalisés par GPS différentiel (Trimble NOMAD; précision moyenne de localisation: 2 m). Les données sont saisies sur le terrain dans le Trimble NOMAD grâce au logiciel TurbovegCE et stockées sur PC dans une base sous Turboveg (Hennekens, & Schaminée, 2001).

Figure 0.5 – Echantillonnage au D-VAC.

Détermination

Les araignées ont été déterminées à l'espèce d'après Roberts (1987) et Roberts (1995). La nomenclature utilisée suit Platnick (2012). Les traits fonctionnels sont basés sur Hänggi et al. (1995) et Harvey et al. (2002) pour les préférences d'habitat et Roberts (1995) et Harvey et al. (2002) pour la taille.
Les carabiques ont été identifiés à l'espèce d'après Coulon et al. (2012), Horellou (2010), Jeannel (1941) et Trautner, & Geigenmüller (1987). La nomenclature des carabiques suit Lindroth (1992). Les traits fonctionnels utilisés sont basés sur Luff (1998) et Bouget (2004). Les tailles utilisées sont tirées de Luff (1998) et Jeannel (1941).
La végétation a été identifiée à l'espèce grâce à Abbayes et al. (1971). Les associations phytosociologiques ont été nommées en suivant la typologie de Foucault, 1984.

Analyses statistiques

Préparation des "variables réponses"

Afin de disposer de données de capture par piège et par unité de temps, les données issues du piégeage par barber ont été divisées par le nombre de jour de piégeage. Les données ont ensuite été loguées (log(n+1) avec n le nombre d'individus capturés par jour) pour rapprocher leur distribution d'une loi normale.
Les données issues des échantillonnages au D-VAC ont été divisées par la surface échantillonnée.
La représentativité de l'échantillonnage quant à la richesse spécifique (diversité α) a été estimée en calculant la moyenne des valeurs de quatre estimateurs : Chao1, Jacknife1, Jacknife2 et Bootstrap. Lorsque la diversité observée était comparable à la diversité estimée, c'est la première qui a été utilisée. Lorsque tel n'était pas le cas, la diversité estimée a été sélectionnée (échantillonnages au D-VAC).
La diversité β peut correspondre à des remplacements d'espèces (turnover) ou des gains/pertes d'espèces (nestedness). Elle a donc été calculée par une matrice de similarité de Sørensen et partitionnée en deux matrices correspondant à ces deux composantes β_t et β_n.
Afin de pouvoir étudier les traits fonctionnels en terme d'abondance et non de fréquence, la moyenne de chaque trait pondérée par l'abondance relative de chaque espèce présentant une valeur de trait a été calculée (CWM). En outre, pour estimer la dissimilarité des traits entre taxa, nous avons calculé une diversité fonctionnelle (FD)en calculant l'entropie quadatrique de Rao.

Analyses préliminaires

Lorsque des séries temporelles étaient analysées, des tests de Box-Pierce ont été menés afin de détecter un éventuel effet saison.
L'autocorrélation spatiale est un phénomène courant en écologie. Elle peut être liée aux relations des invertébrés avec des facteurs environnementaux (sol, végétation...) eux-mêmes autocorrélés. Elle peut aussi être liée à des des comportements tels que les déplacements, la territorialité... (Sanderson et al., 1995; Wagner, 2004). L'autocorrélation spatiale a été systématiquement recherchée grâce à des tests de Moran (I).
Au-delà de l'autocorrélation spatiale, la recherche de patterns spatiaux au sein des variables réponses a été menée par la méthode "Moran's eigenvector maps" (MEM) (Legendre et al., 2013). Les patterns spatiaux recherchés reflètent la connectivité entre sites.

Analyses multivariées

La recherche de variables environnementales influençant les assemblages d'espèces a été menée par analyses canoniques de redondance (RDA). Le choix entre RDA et analyse canonique des

corrélations (CCA) a été fait au préalable selon la longueur des gradients d'une analyse des correspondances redressée (DCA). La RDA est une méthode d'ordination sous contraintes qui est une extension de la régression linéaire multiple à une réponse multivariée. Nos données contenant un nombre important de singletons ou d'espèces rares, nous avons choisi de suivre les recommandations de Legendre, & Gallagher (2001) afin de limiter le poids de ces dernières. Ainsi les données d'abondance d'espèces sont transformées en matrice de distance avant d'être analysées par RDA.
Lorsque l'objectif était d'expliquer, par leur composition spécifique, l'appartenance de relevés à des groupes pré-définis, nous avons utilisé une analyse discriminante descriptive (CDA). Cette dernière permet de construire des facteurs (combinaisons linéaires des indicatrices de ces descripteurs) permettant de discerner les classes.
La régression des matrices de dissimilarité (diversité β) en fonction d'une matrice de variable explicative a été réalisée grâce à une analyse en coordonnées principales (CAP).
Lorsqu'il s'agissait de regrouper des relevés en fonction de leur composition spécifique, des analyses TWINSPAN ont été mises en œuvre. Ce type d'analyse réalise une classification hiérarchique dichotomique d'une matrice de relevés. Cette méthode est très largement utilisée pour les analyses de végétation et particulièrement pour la phytosociologie. La pertinence de la classification peut ensuite être testée par PERMANOVA.
Les comparaisons entre assemblages ont été réalisées par analyse de similarité (ANOSIM). L'ANOSIM permet de comparer les variations d'abondance et de composition spécifique entre unités d'échantillonnage.
La recherche d'espèces indicatrices a été réalisée en utilisant la méthode de Dufrêne, & Legendre (1997) (IndVal) qui combine l'abondance relative d'une espèce et sa fréquence relative L'indice est maximal lorsque tous les individus d'une espèce sont trouvés dans un seul groupe et lorsque cette espèce apparaît dans tous les sites appartenant à ce groupe.

Modèles linéaires et non linéaires

Afin de mettre en évidence des liens entre richesse spécifique ou abondance d'arthropodes et variables prédictives, nous avons utilisé des modèles linéaires généralisés (GLM). Ces modèles sont une généralisation de la régression linéaire multiple permettant de tester des variables réponses présentant des distributions des résidus non normales. La sur-dispersion des données de comptage nous a amené à choisir des distributions de "quasi-Poisson" pour l'ensemble des GLM. La sélection des variables conservées dans les modèles s'est faite par stepAIC. Il s'agit d'une sélection pas à pas basée sur le critère AIC (Akaike, 1974). L'utilisation de ce type de sélection est très controversée mais reste l'une des plus couramment utilisée en écologie. Il convient de souligner que la méthode n'a pas pour objectif de sélectionner les variables significatives mais de sélectionner le modèle le plus parcimonieux. Plusieurs types de modèles ont été testés lors des régressions multiples: linéaire,

logarithmique, inverse, quadratique, cubique, power, compound, logistique, growth et exponentiel. Le modèle avec le meilleur R^2 était sélectionné.
Lorsque les modèles comprenaient un appariement spatial ou temporel, nous avons utilisé des analyses de variances à mesures répétées (R-ANOVA). Ces analyses permettent de prendre en compte la non indépendance des mesures réalisées plusieurs fois sur un même site (appariement temporel) ou sur des sites proches (appariement spatial). Elles ont toutefois été utilisées dans des cadres différents. Dans le chapitre 3, l'objectif est de comparer l'évolution dans le temps des répliquats d'une parcelle par rapport à une autre. On s'intéresse donc à l'interaction entre le facteur fixe (mode de gestion) et le facteur d'appariement. Dans le chapitre 5, on souhaite comparer des paires de parcelles appariées spatialement mais présentant des traitements (gestions) différents. C'est donc l'absence d'interaction qui est recherchée afin de pouvoir réaliser les comparaisons.
Afin d'être en mesure de quantifier les contributions relatives de groupes de facteurs, nous avons réalisé des partitions des variances sur des régressions multiples lorsqu'une seule variable était à expliquer ou sur une CAP lorsqu'il s'agissait de matrices.

Analyses cartographiques

La cartographie des habitats prairiaux a été réalisée grâce à une classification supervisée "orientée pixels" (par opposition à la classification "orientée objet"). Ce choix a été fait car nous souhaitions être en mesure d'estimer l'hétérogénéité spatiale des habitats, ce que ne permettent pas les classifications "orientées objet" ayant pour vocations de "gommer" cette dernière. Nous avons par ailleurs choisi de réaliser nos classifications à partir de sites d'apprentissage classifiés selon la méthode phytosociologique en s'appuyant sur les travaux de Zak, & Cabido (2002) et Fanelli et al. (2005). Le nombre de sites d'apprentissage a volontairement été restreint afin de limiter la variation intra-classe incluse, la classification des sites d'apprentissage étant elle-même très précise (variante d'association). L'hétérogénéité spatiale a été estimée en suivant la méthode proposée par Rocchini et al. (2012) : un indice de Shannon est calculé pour des fenêtres de calculs de tailles variables.

Synthèse des échantillonnages réalisés

Le tableau 0.1 présente l'ensemble des échantillonnages abordés dans ce manuscrit. Le détail des variables environnementales mesurées, abiotiques et biotiques, est donné dans chaque chapitre.

Table 0.1 – Synthèse des échantillonnages réalisés.

Chapitre	Groupe	Variables réponse	Facteurs explicatifs	Méthode d'échantillonnage	Période	Nb relevés / répliquats
1	Araignées Carabiques	Activité-densité Richesse spécifique	Indices de végétation	Barber	05/05/11 à 24/06/11	57
2	Arthropodes (famille) Araignées (espèces) Carabiques (espèces)	Activité-densité Richesse spécifique Peuplements	Temps Paysage	Barber	18/05/12 à 18/06/12	542
3	Araignées Carabiques	Activité-densité Richesse spécifique Diversité fonctionnelle	Date de fauche court et long terme	Barber	05/05/11 à 31/08/11	471
4.	Végétation	Cartographie d'habitat	Humidité Gestion	Phytosociologie	Mai-juin 2011,2012,2013	578
5	Araignées Carabiques Végétation	Activité-densité Richesse spécifique	Date de fauche Fertilisation	D-VAC Phytosociologie	27/05/13 à 28/07/13	430
6	Araignées Carabiques	Densité Richesse spécifique	Variables locales Variables paysagères	D-VAC	27/05/13 à 28/07/13	441

Description des assemblages récoltés

L'ensemble des relevés réalisés a permis d'échantillonner 35 558 araignées (dont 22 625 adultes) appartenant à 21 familles pour un total de 143 espèces (liste taxonomique en Annexes, Table 1). Les effectifs sont largement dominés par les Lycosidae (66,1%) et les Linyphiidae (22,1%). Ces dernières constituent cependant la famille la plus diversifiée avec 51 espèces. Concernant les carabiques, 16 092 individus ont été collectés représentant 21 tribus (liste taxonomique en Annexes, Table 2). Les effectifs sont dominés par les Harpalini (49,8%) et les Pterostichini (30,1%). Les Harpalini sont la tribu la plus diversifiée avec 38 espèces. Lors de l'échantillonnage lié à la recolonisation après crue, 5 372 invertébrés (hors araignées et carabiques) appartenant à 50 familles ont été récoltés (liste taxonomique en Annexes, Table 3). Enfin 249 espèces de plantes appartenant à 38 familles ont été inventoriées (liste taxonomique en Annexes, Table 4). Les Poaceae sont la famille la plus diversifiée avec 43 espèces.

Figure 0.6 – Les deux espèces les plus fréquentes: à gauche *Pardosa prativaga*, à droite *Harpalus rufipes*.

Première partie

Structuration des assemblages d'araignées et de carabiques à l'échelle locale

Contrôle "bottom-up" de la diversité des arthropodes terrestres

Cette section est présentée sous la forme d'un article sous presse dans la revue *Insect Conservation and Diversity*:
Lafage D., Secondi J., Georges A., Bouzillé J-B., & Pétillon, J. (2014). Satellite-derived vegetation indices as surrogate of species richness and abundance of ground beetles in temperate floodplains. *Insect Conservation and Diversity*, sous presse. doi: 10.1111/icad.12056

1.1 Résumé

Les variables d'habitat affectant les assemblages d'araignées et carabiques à l'échelle locale sont nombreuses et incluent, entre autres, des facteurs liés à la végétation (épaisseur de litière, structure de végétation, composition spécifique) et au sol (humidité, température...).
Le rôle de la biomasse végétale semble moins clair et deux théories s'opposent actuellement : la "taxonomic diversity hypothesis" et le "bottom-up control of animal diversity". La première suppose que la diversité végétale est directement corrélée à celle des herbivores, elle-même corrélée à celle des prédateurs. La seconde théorie suppose que c'est la hausse de la biomasse végétale qui permet celle de la diversité de phytophages, cette dernière entraînant une hausse de la diversité de prédateurs.
Dans cette étude, nous avons testé l'influence de la biomasse végétale sur la richesse spécifique et la densité de deux groupes de prédateurs (araignées et carabiques) dans les prairies inondables de l'Île Saint-Aubin (Basses Vallées Angevines, France). La biomasse végétale a été estimée grâce à l'utilisation d'indices de végétation dérivés d'images satellites SPOT.
Au total, 5065 carabiques (63 espèces) et 9969 araignées (42 espèces) ont été capturés et identifiés à l'espèce. Les assemblages d'espèces des deux groupes étaient expliqués par la hauteur maximale de végétation, l'épaisseur de litière et la richesse spécifique en plantes. Les deux indices de végétation testés, Normalised Difference Vegetation Index (NDVI) et Enhanced Vegetation Index (EVI2) étaient fortement corrélés à la richesse spécifique et l'abondance de carabiques. De plus, ces indices étaient négativement corrélés à la diversité spécifique de la végétation, mettant ainsi en évidence l'existence d'un "bottom-up control" de la diversité des carabiques.

L'EVI2 s'est révélé être le meilleur prédicteur de la diversité de carabiques et constitue, à ce titre, un outil à faible coût pour la cartographie et le suivi des assemblages d'arthropodes à large échelle. Il pourra aussi être utilisé dans le cadre de modélisations de répartition et donc de définition de zones de conservation prioritaires, les carabiques constituant un groupe dit "clé de voûte".

1.2 Satellite derived vegetation indices as surrogate of species richness and abundance of ground beetles in temperate floodplains

Abstract

Remotely sensed data are frequently employed for monitoring vegetation and for estimating herbivore diversity. Their use for predicting predator arthropod species abundance and richness has also been investigated with success for ants and beetles in forests using NDVI and for beetles in mountain forests using LiDAR data.
We investigated whether vegetation indices, derived from multispectral SPOT imagery could predict abundance and species richness of ground active spiders and ground beetles in a new ecological context, the floodplain meadows of the Loire River in Western Europe. Using pitfall traps we collected carabids and spiders in the field.
Maximum vegetation height, litter-depth and plant species richness best explained species assemblages of both groups (multivariate analyses). NDVI and EVI 2 were strongly related to activity-density and species richness for ground beetles only, EVI 2 being the best surrogate. Relationships between vegetation indices and spider assemblage patterns were either non significant or weak.
We demonstrated that EVI 2 is a good surrogate of the abundance and richness of carabid species in a temperate floodplain, and has potential as a low cost method for mapping arthropod assemblages at large spatial scales.
Our approach provides a tool which contributes to biodiversity assessment at large spatial scales. It can also contribute to the prioritization of conservation areas and early change detection, as carabids are keystone indicators.

Introduction

One current challenge in conservation biology is to assess and monitor biodiversity over coarse spatial scales. Several indices derived from satellite imagery provide relatively cost-efficient solutions to achieve this goal. The Normalized Difference Vegetation Index (NDVI) is one of the most used of those (reviewed in Pettorelli et al., 2011). NDVI depends on the reflectance peak of vegetation in the infra-red (Tucker, & Sellers, 1986). It is highly correlated with photosynthetically

active radiation absorbed by the plant canopy, photosynthetic capacity, net primary production, leaf area index (LAI), fraction of absorbed photosynthetically active radiation, carbon assimilation and evapotranspiration (e.g. Buermann et al., 2002; Wang et al., 2005). It thus constitutes an informative proxy to monitor photosynthesis over time, and perform temporal and spatial vegetation surveys (Myneni et al., 1997). A refined form of NDVI is now being used: the enhanced vegetation index (EVI) and its adaptation for SPOT images (EVI 2). EVI and EVI 2 were developed to optimize the vegetation signal (because they are less sensitive to saturation with high biomass and to vegetation background) and to reduce atmosphere influences (Huete et al., 2002).

Furthermore, spectral vegetation indices have proved useful to predict changes in herbivore (e.g. African ungultates: Pettorelli et al., 2009) and non-herbivore (e.g. brown bears: Wiegand et al., 2008) vertebrate distribution, abundance and life history traits (Pettorelli et al., 2011), the distribution of invertebrate disease vectors (Daniel et al., 1998) or pests in grasslands, forests and crops (Dreiser, 1994; Brewster et al., 1999). So far, very few studies have investigated the predictive capacity of NDVI for ground-dwelling non-herbivore arthropods. Jiménez-Valverde, & Lobo (2006) modelled *Macrothele calpeiana* (Araneae, Hexathelidae) distribution in Spain but found no influence of NDVI. However, two studies reported positive relationships in ants (Lassau et al., 2005) and carabids (Lassau, & Hochuli, 2008) in Australian forests. Investigations are now focusing on the predictive power of airborne laser scanning (light detection and ranging: LiDAR). Müller, & Brandl (2009) demonstrated the high predictive power of LiDAR-derived variables for beetles' assemblages and Vierling et al. (2010) for spiders. Despite its efficiency, LiDAR technology remains expensive in comparison with multispectral imagery acquisition, thus limiting its applications for large areas. The goal of our study was to test whether NDVI and EVI 2 derived from multispectral images are good predictors of carabid and spider abundance and diversity in a a new habitat: the temperate floodplain grasslands of Western Europe.

Material and methods

The study site is located near Angers, Western France (Long:0 ° 32'37.7"W Lat: 47 ° 30'05.6"N). It is a 600 Ha island circled by three rivers that is flooded about 3 months each year. Land cover is dominated by hay meadows and to a lesser extent by poplar groves. Grasslands are cut in summer and grazed in autumn. Arthropods were sampled on five parcels, four (A,B,C,D covering respectively 2.9 Ha, 1.4 Ha, 1.9 Ha, 1.2 Ha) of which were under an agri-environmental scheme which delays mowing to a fixed date and one (E covering 0.4 Ha) which has been left unmanaged for 20 years (Figure:1.1). Sampling was performed from May to June 2011, before the first mowing took place. This period corresponds to the peak of vegetation productivity in our study system. We set 10 pitfall traps (100 mm diam.) per parcel that were located at least 20 m from parcel edges and regularly distributed following a grid pattern (20 m apart) to avoid respectively edge effects and interaction between traps (Topping, & Sunderland, 1992). Pitfall traps were filled with preservative solution (50% monoethylene glycol, 50% water) and emptied every two weeks (3 times during the sampling period).

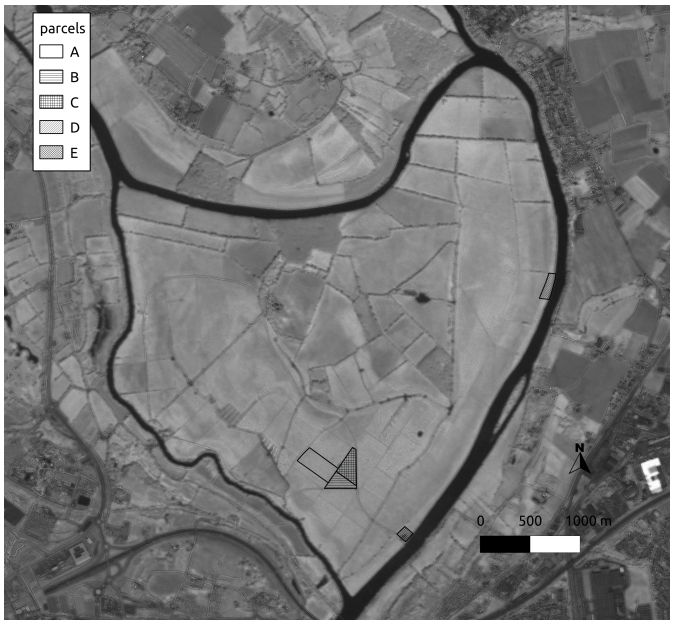

Figure 1.1 – Cartography of the study site with parcels sampled. Background is a grayscale SPOT image.

Phytosociological data were recorded in June in a 1 m^2 quadrat around each trap using the Braun-Blanquet (1928) method: within each plot, a cover value was attributed to each plant species following the Braun-Blanquet scale. Maximum vegetation height, height of the dominant vegetation layer and litter depth were measured to the nearest centimeter. Soil conductivity, moisture and temperature were measured in May and June using a W.E.T. sensor (5 cm deep) connected to

a moisture meter HH2 (both built by Delta-T Devices Ltd., Cambridge, UK). Two measurements within each quadrat were carried out.

One SPOT 5 HRG image (©CNES 2011 and 2012, Distribution Spot Image S.A.) with 3 bands (green, red, near infra-red) was acquired on the 24th May 2011. To respect the rule stating that pixels should be 2 to 5 times smaller than the area of objects of interest (O'Neill et al., 1996), we selected a product with 2.5 m resolution. The image was obtained from a pan-sharpened image (2.5 m resolution) and a multispectral image (10 m resolution). Pre-treatment of images was carried out by the CNES (Centre National d'études Spatiales). It includes geometrical correction, radiometric correction of distortions due to differences in sensitivity of the elementary detectors of the viewing instrument, geometric correction of systematic effects (panoramic effect, Earth curvature and rotation) and radiometric distortion geometry. Atmospheric correction of the image was not realised.
NDVI and EVI 2 were computed using Grass GIS software 6.4.1 (GRASS Development Team, 2012) applied to a SPOT image (2.5 m resolution, 3 bands) acquired on the 24th May 2011. NDVI is defined as:

$$NDVI = \frac{(R_{NIR}-R_{red})}{(R_{NIR}+R_{red})}$$

EVI 2 is defined as:

$$EVI2 = 2.5\frac{(R_{NIR}-R_{red})}{(R_{NIR}+2.4(R_{red}+1))}$$

where R_{NIR} and R_{red} refer to the reflectance values derived from spectral radiances measured by the near-infrared channel and the red visible channel, respectively. NDVI and EVI2 range from -1 (deep water) to 1 (maximum vegetation greenness).

To analyze the patterns of species composition, multivariate analyses were performed on activity-densities of each species ($log(n+1)$ with n being the number of individuals captured per day and per trap; referred as 'abundance' thereafter). Following Legendre, & Gallagher (2001), species activity-densities were transformed to a Bray-Curtis distance matrix prior to a redundancy analysis (RDA). In the RDA, the distance matrix was the response variable and the environmental variables were the predictors. A forward selection procedure was used to select the environmental variables explaining the most variance in the Bray-Curtis distance matrix. Monte Carlo tests with 999 permutations were carried out to test the significance of the selected environmental factors and RDA axes.
Phytosociological relevés were classified by Two-Way Indicator Species Analysis, TWINSPAN (Hill, 1979) under JUICE software (Tichý, 2002). Classification was carried out following the typology

proposed by Foucault (1984) to the alliance level. Each alliance corresponded to a parcel type.

To evaluate the ability of vegetation indices to predict arthropod assemblages (total activity-density and species-richness) we used analyses of covariance (ANCOVA). Species richness and activity-density were response variables, 'type of parcel' categorical fixed factor, and NDVI or EVI 2 continuous covariate (Model 1; García-Berthou 2001). If the interaction between 'type of parcel' and NDVI or EVI 2 was not significant, a Model 2 ANCOVA assuming homogeneity of slopes was performed. If the interaction was significant, the data from both types of parcels were analysed separately with respect to their NDVI or EVI 2 (Model 3). When interaction was not significant and NDVI or EVI 2 was significant, a linear regression was performed with NDVI and EVI 2 as explanatory variable. Statistics were computed using R software 2.14.1. (R Development Core team, 2013). Models with lower Akaike information criterion (AIC) scores were selected (Akaike, 1974).

Results

A total of 5065 adult carabids and 9969 spiders (7431 adults) belonging to 63 and 42 species respectively were collected. Two carabid species *Poecillus cupreus* (Linaeus, 1758) and *Harpalus ruffipes* (De Geer, 1774) accounted for more than 51% of carabids. Among spiders, Lycosidae were highly dominant (83,8% of individuals) followed by Thomisidae (5.6%). One species accounted for 54,8% of individuals: *Pardosa prativaga* (Clerk, 1757). NDVI values ranged from 0.17 to 0.255. EVI 2 values ranged from 0.27 to 0.50.

Only the first RDA axis was significant for carabids ($F_{1,42} = 17.90, P = 0.005, 81.7\%$ of total inertia explained) and for spiders ($F_{1,42} = 11.82, P = 0.005, 80.1\%$ of total inertia explained). They segregated sites according to litter depth and number of plant species for carabids (Figure 1.2) and to maximum vegetation height and number of plant species for spiders (Figure 1.2). Maximum vegetation height and litter depth contributed positively to axis 1, and number of plant species negatively (Figure 1.2).

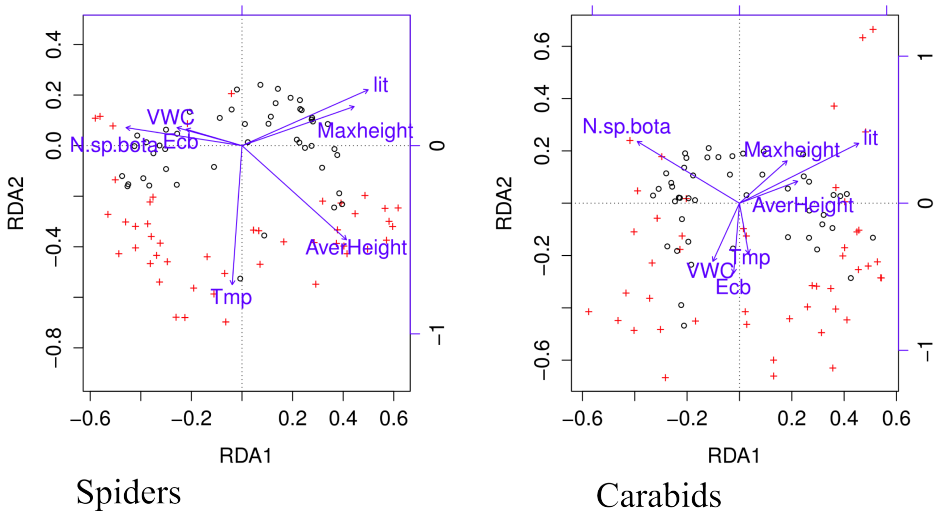

Figure 1.2 – RDA on spider and carabid beetle species Bray-curtis distances. Sites are represented by crosses and species by circles. N.sp. Bota: Plant species richness; MaxHeight: Maximum height of vegetation; AverHeight: Height of dominant vegetation layer; lit: Litter depth; Tmp: Soil temperature; VWC: soil humidity; ECb: soil conductivity.

Twinspan analysis on vegetation relevés distinguished two groups of parcels. One (A, B, C) belonged to *Oenanthion fistulosae* (Foucault, 1984), the second, (D and E (unmanaged)) to *Bromion racemosi* (Tüxen, & Preising, 1951).

Best AIC scores were obtained with EVI 2 for all models (Table 1.1) so we present only results for this index. For carabid beetles, we detected no significant interaction between EVI 2 and parcel type ($F_{2,46} = 0.24, P = 0.626$) (Table 1.2), a significant effect of parcel type ($F_{1,47} = 5.52, P = 0.023$) and a positive relationship between EVI 2 and activity-density ($F_{1,47} = 85.54, P < 0.001$). Linear regression demonstrated a strong positive association between EVI 2 and carabid beetle activity-density (Figure 1.3) ($P < 0.001, R^2_{adj.} = 0.61$).

Table 1.1 – AIC scores of models. A: Activity-density; S: Species richness.

Dependant variables	Explicative variables	AIC
A carabids	NDVI	−83.25
	NDVI + Parcel type	−92.46
	EVI 2	-88.9
	EVI 2 + Parcel type	−94.23
S carabids	NDVI	248.7
	EVI 2	242.5
A spiders	NDVI	−35.9
	EVI 2	−36.12
S spiders	NDVI	228.8
	EVI 2	229.9

A slightly different result was found for species richness (Table 1.2). We found no significant interaction between EVI 2 and parcel type ($F_{2,46} = 1.152, P = 0.289$), no effect of parcel type ($F_{1,47} = 0.13, P = 0.72$) and a positive relationship with EVI 2 ($F_{1,47} = 37.15, P < 0.001$). Linear regression demonstrated a lower, but still significant, positive association between EVI 2 and species richness ($P < 0.001, R^2_{adj.} = 0.42$) (Figure 1.4).

Table 1.2 – ANCOVA and linear regressions on spider and carabid abundance (A) and species richness S). In ANCOVA F, P and R^2 values for parcel type and EVI 2 are given for model 2 (standard ANCOVA) as the interaction between EVI 2 and parcel type was not significant.

		ANCOVA		Linear regression with EVI2	
Dependant	Interaction	Independent variables			
variables	EVI 2 / Parcel type	Parcel type	EVI 2	Test	Model
A carabids	$F_{2,46} = 0.24$; $P = 0.626$	$F_{1,47} = 5.52$; $P = 0.023$	$F_{1,47} = 85.54$;$P < 0.001$	$P < 0.001$ $R^2_{adj.} = 0.61$	$1.49 * EVI2 - 0.09$
S carabids	$F_{2,46} = 1.15$;$P = 0.289$	$F_{1,47} = 0.13$; $P = 0.722$	$F_{1,47} = 37.15$; $P < 0.001$	$P < 0.001$ $R^2_{adj.} = 0.42$	$28.81 * EVI2 - 0.40$
A spiders	$F_{2,46} = 3.74$; $P = 0.060$	$F_{1,47} = 0.65$; $P = 0.426$	$F_{1,47} = 5.16$; $P = 0.028$	$P = 0.028$ $R^2_{adj.} = 0.07$	$0.67 * EVI2 + 0.48$
S spiders	$F_{2,46} = 0.08$; $P = 0.784$	$F_{1,47} = 0.00$; $P = 0.996$	$F_{1,47} = 5.48$; $P = 0.024$	$P = 0.023$ $R^2_{adj.} = 0.08$	$9.76 * EVI2 + 7.13$

For spider activity-density, we detected no significant interaction between EVI 2 and parcel type ($F_{2,46} = 3.74, P = 0.289$), no effect of parcel type ($F_{1,47} = 0.65, P = 0.426$) and a significant relationship with EVI 2 ($F_{1,47} = 5.16, P = 0.028$) (Table 1.2). For spider species richness, we found no interaction between parcel type and EVI 2 ($F_{2,46} = 0.08, P = 0.784$), no effect of parcel type ($F_{1,47} = 0.00, P = 0.996$) and a significant relationship with EVI 2 ($F_{1,47} = 5.48, P = 0.024$). Linear regressions showed significant but weak associations between EVI 2 and activity-density and species richness for spiders ($P = 0.07, R^2_{adj.} = 0.07$ and $P = 0.08, R^2_{adj.} = 0.08$, respectively).

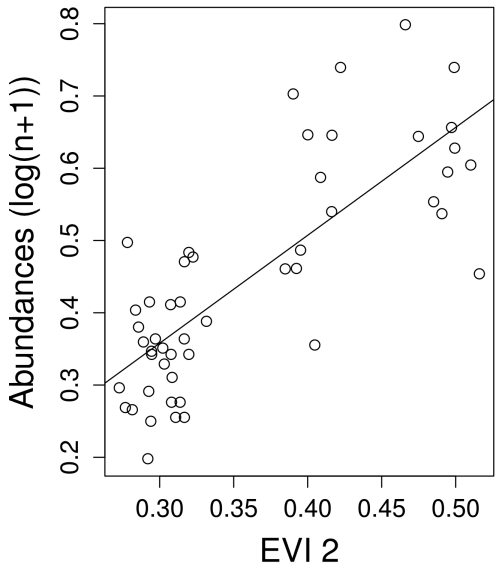

Figure 1.3 – Relationship between abundance and EVI 2 in carabid beetles. Line corresponds to the linear regression model.

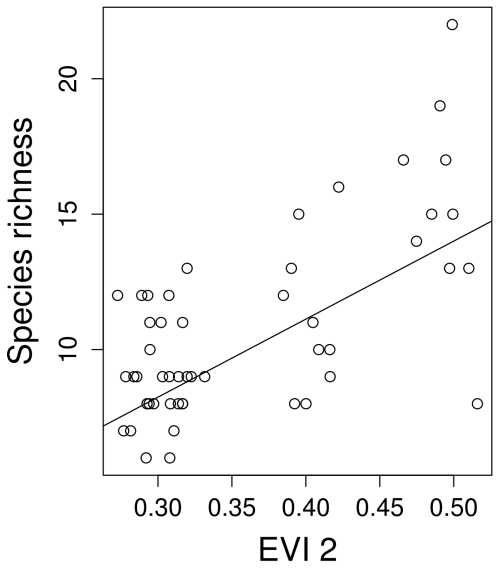

Figure 1.4 – Relationship between species richness and EVI 2 in carabid beetles. Line corresponds to the linear regression model.

Discussion

We found a strong positive association between vegetation indices and carabid activity-density and species richness as Lassau, & Hochuli (2008) did on forest carabids with NDVI. Best results were obtained with EVI 2 probably because this index is less sensitive to atmospheric perturbations. This positive association contradicts the well documented assumption that catches of Carabidae are greater in sparse than in dense grassland stands (e.g. Honek, 1988). This relationship could be explained by the 'bottom-up control of animal diversity' hypothesis (Siemann, 1998). The theory states that an increase in plant productivity may induce an increase in herbivore diversity by (1) increasing the activity-density of rare resources ('resource rarity hypothesis'), (2) increasing herbivore activity-density and local persistence ('consumer rarity hypothesis') or (3) increasing intraspecific density dependence ('density dependence hypothesis') (Siemann, 1998). Increasing the diversity of herbivores can finally increase the diversity of predators (Siemann, 1998). The positive but very weak associations between EVI 2 and spider species richness and activity-density ($R^2 < 0.10$) prevent us from considering EVI 2 as a surrogate of spider diversity. These results, in accordance with Jiménez-Valverde, & Lobo (2006), may be explained by the higher trophic level in spiders than in carabids (Girard et al., 2011).

Litter depth and number of plant species best explained carabid species composition and maximum vegetation height and number of plant species best explained spiders species composition

in our study area. Carabids are usually considered dependent on several abiotic and biotic factors, including (1) temperature or humidity, (2) food conditions, (3) presence and distribution of competitors, and (4) life history and season, including migration between hibernation and reproduction habitats (Lövei, & Sunderland, 1996). In our study, assemblages of species were not related to temperature or humidity because of the small size of the study area, but this link may be difficult to demonstrate for all the population, as seasonal dynamics vary between species (Honek, 1997). Also, soil temperature was measured only twice during our study (to evaluate synchronic differences in assemblages among traps, and not with temporal changes), which was probably not sufficient to accurately assess the influence of this parameter on spiders and ground beetles.

It has been hypothesized that taxonomic diversity of plant species is directly correlated with the diversity of herbivores (the 'taxonomic diversity hypothesis') because to each additional plant species corresponds specialized consumers (e.g. Siemann, 1998). These effects might cascade up from plant diversity via herbivore diversity to predator diversity (Hunter, & Price, 1992). In our case, plant species-richness was highly negatively correlated with EVI 2 and thus to species richness of carabid beetles. This could be explained by the presence of competitive plant species. In grasslands plant communities, highly competitive species (in our case *Elytrigia repens* and *Agrostis stolonifera*) reduce diversity and increase biomass (i.e. an increase in EVI 2) (Amiaud et al., 2008). The 'Taxonomic diversity' (e.g. Siemann, 1998) and 'bottom-up control of animal diversity' (Siemann, 1998) hypotheses seem to reject each other in the floodplain grasslands studied.

Habitat variables that usually affect ground dwelling spider assemblages are litter depth (e.g. Lawrence, & Wise, 2004), vegetation structure (e.g. Downie et al., 1995), plant species composition (Dennis et al., 2001) and soil moisture content (Entling et al., 2007). Plant species-richness and the maximum height of vegetation are the two explanatory variables here. The positive association between EVI 2 and activity-density and species richness of spiders is significant but very weak. These results are in opposition with the assumption that catches of Lycosidae (the highly dominant family in our study) are greater on sparsely rather than densely vegetated ground (Honek, 1988).

Many studies have investigated relationships between arthropods and the abiotic environment (e.g. Lessard et al., 2011; Sinclair et al., 2006) but few studies specifically compared spiders' and carabids' responses to abiotic factors. Pétillon et al. (2008) demonstrated a similar positive response to soil moisture in both groups. In contrast, carabids showed no response to vegetation variables and litter depth, whereas spiders did. Our results are partly in opposition with those of Pétillon et al. (2008) as we did not find any effect of soil moisture on carabids and spiders. Both groups were sensitive to vegetation structure (maximum vegetation height for spider and litter-depth for carabids). Biases in capture efficiency of traps are reported in the literature. Indeed, high density vegetation reduces the mobility of ground-dwelling arthropods (Thomas et al.,

2006) and might thus decrease the efficiency of the pitfall traps in densely vegetated habitats. In our case, catches were more numerous in high densely vegetated plots despite this possible bias. So, the bias in sampling efficiency caused by indirect effects of management (spatial variations of vegetation density) seems negligible or absent and specimens were really more numerous in densely vegetated plots.

In conclusion, EVI 2 can be used to estimate activity-density and species richness of carabids in floodplains. Considering the relatively low cost and increasing availability of multispectral images, EVI 2 seems to be a useful proxy of carabid populations over large areas. Remotely sensed imagery also allows plant diversity assessment (Rocchini et al., 2007). Thus, EVI 2 could contribute to multitaxa biodiversity assessment and monitoring over large areas which meet the current demands of managers. It could also be used in prioritizing conservation areas and early change detection, as carabids are considered as keystone indicators (group of species affecting its environment and therefore other species disproportionately strongly relative to its abundance Mills et al., 1993).

Chapitre 2

Processus de recolonisation des prairies après crue

Cette section est présentée sous la forme d'un article soumis à la revue *Ecohydrology*:
Lafage D., Papin C., Secondi J., Canard A., & Pétillon, J. Short term resilience of arthropod assemblages after a spring flood, with focus on spiders (Arachnida: Araneae) and carabids (Coleoptera: Carabidae). *Ecohydrology*, soumis.

Figure 2.1 – Grand Prée de Rochefort. Crue de printemps. Juin 2013.

2.1 Résumé

Le rôle prépondérant des crues en tant que facteur de forçage des assemblages d'espèces a été démontré sur plusieurs groupes d'arthropodes. Cependant la plupart des études se situent dans des contextes de crues régulières et prévisibles (zones tropicales ou crues hivernales en Europe). Les capacités de résilience et de recolonisation des communautés après des crues de printemps ou estivales ont été bien moins étudiées de par la difficulté de disposer de données antérieures à la crue et de mise en œuvre des échantillonnages. Or, dans un contexte de réchauffement climatique, la fréquence des crues exceptionnelles sera amenée à augmenter. Il est donc crucial de mieux comprendre les phénomènes qui régissent la recolonisation des milieux après ce type de crue.
Dans cette étude, nous avons étudié les changements intervenant au cours du temps après une crue de printemps survenue sur les prairies de fauche inondables de l'Île Saint-Aubin (Basses Vallées Angevines, France). Les échelles d'investigation étaient la communauté d'arthropodes (échelle de la famille) ainsi que les communautés de deux groupes de prédateurs (araignées et carabiques à l'échelle de l'espèce). Nous avons aussi étudié l'influence des éléments paysagers sur la recolonisation.
Au total, 14 767 arthropodes (87 familles) dont 5 538 araignées (55 espèces) et 3 396 coléoptères carabiques (66 espèces) ont été capturés.
Les analyses multivariées ont mis en évidence l'existence d'assemblages différents entre sites inondés et jamais inondés et ont permis de suivre l'évolution temporelle après crue des assemblages des sites inondés. Les arthropodes, à l'exception des lycoses et dans une moindre mesure de certaines espèces de carabiques, recolonisent lentement le milieu après la crue. Les assemblages d'araignées retrouvent des caractéristiques proches de celles des sites non inondés beaucoup plus rapidement que les carabiques. Enfin, nous avons démontré l'importance de la présence de haies dans le processus de recolonisation. Ces dernières servent probablement de refuges aux espèces colonisant par déplacement au sol mais jouent aussi un rôle de barrière pour les espèces ayant un mode de colonisation aérien.

2.2 Short term resilience of arthropod assemblages after a spring flood, with a focus on spiders and carabids

Abstract

Despite the expected increase in extreme flood frequency, the manner in which terrestrial arthropods cope with regular submersion of their habitat remains poorly understood in meadows, especially in temperate floodplains. Here, we studied the recolonisation dynamic of arthropods after a severe spring flood in the Loire Valley (France). We carried out analyses at the community (order or family identification level) and species scales, focusing on the assemblages of two dominant

and diverse groups: carabids and spiders. Our objectives were (i) to describe the temporal changes in community structure after flooding, and (ii) to assess the influence of landscape configuration on recolonisation patterns of species and their functional traits. Fieldwork was performed along three sampling transects, by using 75 pitfall traps in 2012. A total of 14,767 arthropods belonging to 87 families were trapped, including 5,538 spiders (55 species) and 3396 carabids (66 species). Multivariate analyses discriminated assemblages from flooded and non-flooded habitats, and revealed changes over time in arthropod families and species after flood withdrawal. In particular, wolf spiders (Lycosidae) were the first to recolonise, whereas other groups clearly avoided flooded sites. Our results also revealed that short distances to hedgerows, and to a lesser extent, distance to woodlands and to non-flooded meadows, favoured the recolonisation of large and ground-running spiders. In conclusion, our study shows the short-term resilience of certain groups or stenotopic species to flooding, and also the relevance of multi-taxon based studies. Consequently, the presence of hedgerows has to be considered carefully in management plans due to their role of refuge during flooding.

Introduction

Natural floodplains are considered as the most species-rich habitats in temperate regions (Gerken, 1988). Indeed, disturbances induced by flooding are an integral component of floodplain ecosystem function (Ward et al., 2001). Flow variations shape the riverbanks (Scott et al., 1997), contribute to their dynamic equilibrium (Junk, 2005), and maintain biodiversity in the floodplains (Adis, & Junk, 2002).

In Europe, large rivers have been highly modified by humans for protection against floods, mainly by building dykes and floodplain drainage. One of the expected effects of climate change is the increased frequency of extreme hydrological events on European rivers (Dankers, & Feyen, 2008). This situation is likely to increase the anthropogenic management of large rivers. Assessing the ability of organisms to recolonise supposedly virgin habitats after flooding, thereby maintaining local biodiversity, is thus essential to the establishment of management strategies that encompass biodiversity conservation.

Resistance and phenological strategies of ground-dwelling arthropods may have evolved before the colonisation of floodplains ('predisposition': Weigmann, & Wohlgemuth-von Reiche D., 1999). However, flood events frequently result in the displacement of interstitial (Marmonier et al., 1992), benthic (Rempel et al., 1999) and terrestrial (e.g. Lambeets et al., 2008) invertebrates, by either passive or active movements. In temperate regions, flooding is not as predictable because of less seasonal precipitation pattern and relatively unpredictable snowmelt (Adis, & Junk, 2002). Flood timing, rather than magnitude, is also believed to determine the impact of floods on organisms (Junk, 2005). Arthropod communities of European rivers are likely to use a "risk strategy" to survive in this naturally disturbed habitat. The strategy consists of a suite of life history traits such

high productivity ("r-strategy"), high capacity for dispersion, and active recolonisation from areas that have been sheltered from flooding (Zulka, 1994). Vertical emigration to uplands or higher vegetation is also expected to increase recolonisation success (Adis, & Junk, 2002). A few terrestrial species also withstand short to prolonged (up to several weeks) periods of submersion (e.g. insects: Hoback, & Stanley 2001, spiders: Pétillon et al. 2009). Conversely, flood events can be seen as a way to colonise new habitats and exchange individuals between distant populations (Lambeets et al., 2010). Strategies used by terrestrial arthropods to cope with the regular submersion of river banks have been widely studied (e.g. Hering et al., 2004; Lambeets et al., 2008), salt-marshes (e.g. (e.g. Pétillon et al., 2009; Sudd, 1972) but were studied to a less extent in natural grasslands.

In this study, we assessed the recolonisation process of grasslands by invertebrates, at both community and species scales, after a late spring flood in the Loire Valley (France). The Loire river is poorly affected by human modifications regarding hydrological functioning, especially when compared to other European large rivers (Descy et al., 2014) and can be considered as a virgin system. We focused on carabids and spiders because these two groups are highly diverse and abundant in floodplains (Ballinger et al., 2007; Lafage et al., 2014b; Lambeets et al., 2008) worldwide.

Although floods occurring in winter and early spring probably have less effect on most organisms than floods occurring in summer (Ilg et al., 2008), we expect arthropod assemblages to change after flooding and to return more or less rapidly to an equilibrium, here estimated by a comparison to assemblages from non-flooded grasslands. Besides, because of their sensitivity to hydrological conditions, they are considered as good indicators of moisture (Greenwood et al., 1991; Greenwood et al., 1995).

Comparison of time response to perturbations suggests that spiders have higher dispersal abilities than carabids (Hendrickx et al., 2007; Lafage, & Pétillon, 2014a). We consequently expected spiders, particularly ground-runners, to be faster recolonisers than carabids and thus to be more resilient. The two groups are also known to react to landscape characteristics and could use landscape elements to escape from floods. Carabids and large spiders are known to climb tree trunks, whereas ballooning spiders (Linyphiidae) are carried into the canopy by airflow (Adis, & Junk, 2002). We hypothesise that increasing distances to refuges have an impact on recolonisation and on functional traits, notably due to interactions between landscape configuration and body size and the dispersal abilities of the two groups. For instance, Andersen (2011) found large carabids to move away from water during winter, whereas small ones did not. Finally, we expected the large ground-dwelling spiders and carabids to be able to retreat into refuges and to recolonise from there, while small ballooning spiders and flying carabids could recolonise from adjacent habitats, and thus, experience little to no influence from the surrounding landscape on recolonisation abilities.

Material and methods

Sampling design

The study site was located in Western France (0 ° 32'37.7" W, 47 ° 30'05.6" N). The study area is an island (600 ha) encircled by three rivers. It is flooded yearly, mainly during late autumn and winter for about three months. Spring floods occur approximately every five years. Average annual river flow in 2012 was 135.8 m^3/s. Three floods occurred during spring 2012: 26 April (185.5 m^3/s), 2 May (399.8 m^3/s) and 22 May (184.8 m^3/s) (Figure 4.1). Land is mainly covered by hay meadows and a few poplar groves. The hedgerow network is poor with a total length of only 22 km. Grasslands are cut in early or mid-summer and grazed by cattle in autumn.

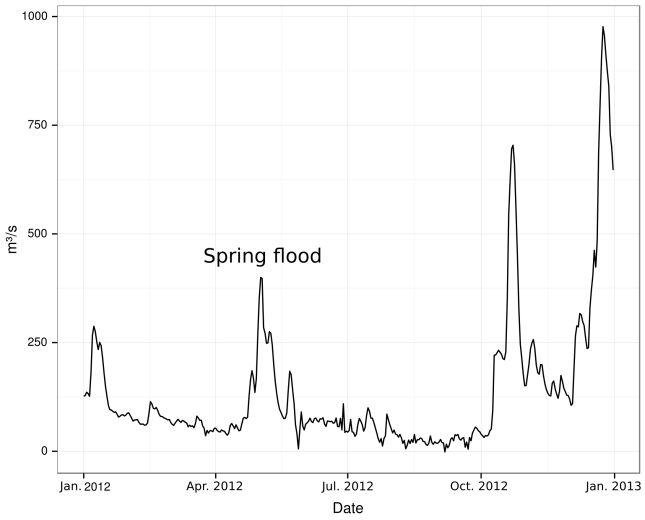

Figure 2.2 – Average daily debit of the River Maine in 2012.

Sampling design was based on vegetation maps produced using remote sensing techniques and topography. Fifteen sampling stations were chosen along three transects following the topographic gradient (five stations per transect, see Appendix 1), with each station comprising five pitfall traps (100 mm diameter). The sampling design was stratified and encompassed six stations located in non-flooded grasslands (three xerophilous and three meso-hygrophilous stations) and nine stations located in flooded grasslands (five meso-hygrophilous and four hygrophilous stations). We hypothesised that xerophilous non-flooded stations provided refuge and sources for post-flood recolonisation, which was tested by comparing their arthropod composition with the arthropod composition at non-flooded meso-hygrophilous stations.

Arthropod sampling was carried out from 18 May to 18 June 2012. Pitfall traps were located at least 20 m apart to avoid interactions between each other, and yielded the calculation of 'activity-density' for ground-dwelling arthropods (Topping, & Sunderland, 1992). Traps were filled with preservative solution (50% monoethylene glycol, 50% water) and emptied every three or four days

for a total of 10 sampling periods.

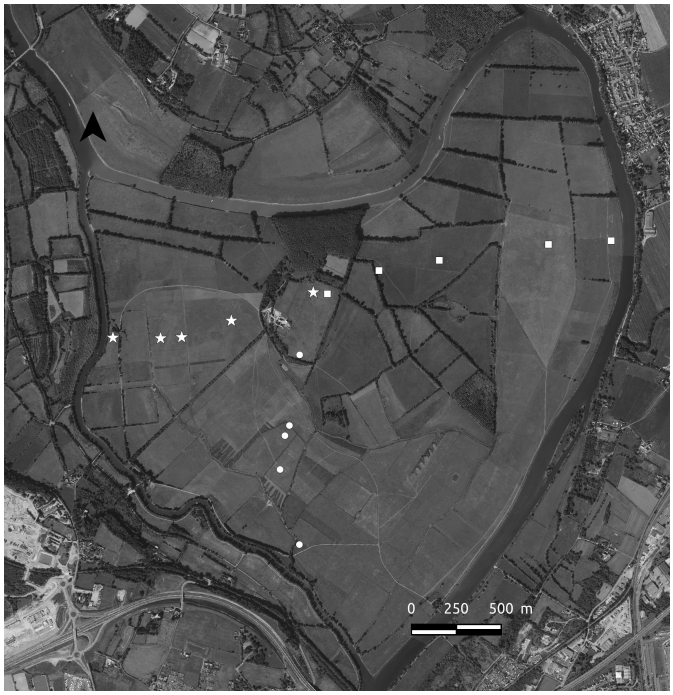

Figure 2.3 – Localisation of the sampling sites along each transect. Each symbol corresponds to one transect.

Arthropod identification and classification

All terrestrial arthropods were identified to family level except springtails (Collembola), mites (Acari) and centipedes (Myriapoda) which were identified to the sub-order level; bees (Apoideae) to super-family level and ants (Formididae) to sub-family level. Arthropods were preserved in 70% ethanol. Adult carabids and spiders were identified to species level. Spider nomenclature follows Platnick (2012). Carabid nomenclature follows Lindroth (1992).
Catches in pitfall traps were divided by trapping duration, in order to calculate 'activity-density' (Sunderland et al., 1995).

Statistical analyses

Prior to analyses, spatial autocorrelation was tested using Moran's I for arthropod, spider and carabid activity-densities and species richness. Autocorrelation was significant (Table 2.1) but low enough to be neglected (Gerisch et al., 2012).

Table 2.1 – Spatial autocorrelation tests (Moran's I values; significativity of tests * = 0.05) and seasonality tests (Box-Pierce tests) for activities-density and species richness of arthropods, spiders and carabids.

	Activity-density	Species richness
Autocorrelation		
Arthropods	I=0.44*	I=0.48*
Spiders	I=0.41*	I=0.46*
Carabids	I=0.40*	I=0.45*
Seasonality		
Arthropods	χ^2=0.46	χ^2=1.33
Spiders	χ^2=0.22	χ^2=0.32
Carabids	χ^2=3.28	χ^2=0.39

Seasonal effect was tested on activity-density and species richness of arthropods, spiders and carabids of non-flooded sites by using Box-Pierce tests.

The short-term recolonisation of assemblages was first studied at the family level on all arthropods using correspondence discriminant analysis (CDA) (Perrière, & Thioulouse, 2003). CDA categorises observations in pre-defined groups. The dependent categorical variable was the class of time after flooding, and the response variable was the activity-density of families. Permutation tests (999 iterations) were used to test class discrimination. Catches were classified according to five flood categories: three classes of time after flooding (1-9 days , 10-19 days, >20 days), and two stations non-flooded (xerophilous and meso-hygrophilous).

We then focused on the short-term resilience of carabid and spider species using CDA with the same categorical variables, but with activity-density of species as explanatory variables. To identify spider and carabid species indicating a particular period in the recolonisation process, we used the approach developed by Dufrêne, & Legendre (1997), which statistically determines the association of a species to one or several groups by defining an indicator value (IndVal). IndVals were first calculated for flooded vs non-flooded sites and then for each of the five flood categories (see above). The enhanced method recommended by De Caceres, & Legendre (2009) was applied using the R package 'Indicspecies' (De Caceres, & Jansen, 2010). Significance of the indicator values was tested using 999-permutations test and Sidak's correction for multiple testing.

Analyses of Similarity (ANOSIM) were then used to test differences in species composition between flood categories for both spiders and carabids, using the R package "vegan" (Oksanen et al.,

2013). The recolonisation process was assessed by testing for some differences in activity-density and species richness between the five flood categories using non parametric Kruskal-Wallis tests followed by two-sample Wilcoxon tests.
In order to test the effect of landscape on the functional composition of spider and carabid assemblages, MANOVAs with Tukey HSD post-hoc tests were used with classes of distance to the nearest potential refuges (minimal distance to hedgerows, woodlands and non-flooded meso-hydrophilous grasslands) as independent explanatory variables and activity-densities per functional trait as response variables. Three classes of distance, chosen to obtain comparable numbers between classes, were used for each landscape variable. For distance to the nearest hedgerow, non-flooded habitat and refuge, distance classes were 0-100 m, 101-200 m and >200 m. For distance to the nearest woodland, distance classes were 0-300 m, 301-600 m and >600 m. Only flooded sites were included in the analysis. Functional traits included dispersal ability and size of carabids and spiders. Functional traits included dispersal ability and size of carabids and spiders, as displacements of these two traits have already been observed on riverbanks in relation to increasing flooding disturbance (Lambeets et al., 2008). Dispersal ability of carabids was estimated by the development of wings in adults (e.g. Hendrickx et al., 2007). Species were classified as macropterous, apterous or dimorphic following Desender et al. (2008). For dimorphic species, wing development was checked on all individuals. Spiders were classified according to their dispersal habits as adults (Uetz et al., 1999): runners vs. ballooners. Carabids were divided into three size classes: small: 0-5 mm, medium: 5-10 mm, large > 10 mm. Spiders were also divided into three size classes: small: 0-3 mm, medium: 3-5 mm, large > 5 mm (Varet et al., 2013b).

Results

We found no seasonal effect on activity-density or on species richness (Table 2.1). Autocorrelation was significant but low enough to be neglected (Gerisch et al., 2012).

Description of assemblages

A total of 14,767 arthropods belonging to 87 families were trapped. Arthropod assemblages were dominated by one spider family (Lycosidae: 30.8% of total catches) and one carabid beetle tribe (Harpalini: 11.4% of total catches). A total of 5,538 spiders (4,674 adults) of 55 species representing 11 families were trapped. Lycosidae were highly dominant (83.4% of individuals). One species accounted for almost 50% of adult individuals: *Pardosa prativaga*. A total of 3,396 adult carabids belonging to 66 species and 17 tribes were collected. Three species (*Poecilus cupreus*, *Harpalus affinis* and *Harpalus dimidiatus*) accounted for more than 40% of individuals.

Change in communities after flooding

The first two axes of the CDA on arthropods explained 71.89% of the total variance. Permutation tests showed that the group discrimination was significant ($P < 0.001$). Assemblages from the flooded xerophilous habitat presented a clearly different species composition (ANOSIM, Table 2.2) and was characterised by Histeridae, Acrididae, Gnaphosidae and Harpalini (Figure 2.4). Assemblages from habitats 1-9, 10-19 and >20 days after flood withdrawal, characterised by Lycosidae (Figure 2.5), presented no significantly different species compositions from each other (ANOSIM, Table 2.2).

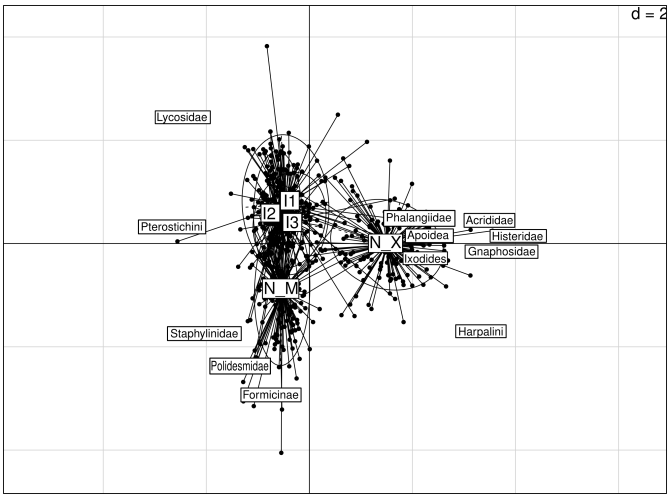

Figure 2.4 – Correspondence Discriminant Analysis of the arthropod groups classified by time class since water withdrawal. Groups presented are the ones that contributed most to the axes. Ellipses represent the summarized weighted scatter plot for each class. 1–9 days (I1), 10–19 days (I2), more than 20 days (I3) since water withdrawal and non-flooded xerophilous (N_X) and meso-hygrophilous (N_M) grasslands.

Non-flooded meso-hygrophilous sites, characterised by the presence of Formicinae, Polydesmidae and Staphylinidae, presented a significantly different species composition from all other classes (ANOSIM, Table 2.2).

The two first axes of the CDA on spiders explained 74.7% of the total variance. Permutation tests showed that the group discrimination was significant ($P < 0.001$). The assemblage from the non-flooded xerophilous stations presented a clearly different species composition (Figure 2.5; ANOSIM: Table 2.2) and was characterised by *Haplodrassus signifer* (confirmed by IndVal=0.52, $P = 0.005$), *Haplodrassus dalmatensis* (confirmed by IndVal=0.45, $P = 0.005$), *Zelotes civicus* (confirmed by IndVal=0.39, $P = 0.005$), *Xysticus kochi* (confirmed by IndVal=0.36, $P = 0.005$) and *Argenna subnigra* (confirmed by IndVal=0.17, $P = 0.005$).

Table 2.2 – Analysis of similarity (ANOSIM) values between stations, 1–9 days (I1), 10–19 days (I2), more than 20 days (I3) since water withdrawal and non-flooded xerophilous (N_X) and meso-hygrophilous (N_M) grasslands, for all arthropods, spiders and carabids.

Group	I1	I2	I3	N_M
Arthropods				
I2	$R = -0.06$, $P = 0.994$			
I3	$R = -0.07$, $P = 0.966$	$R = 0.02$, $P = 0.160$		
N_M	$R = 0.14$, $P = 0.001$	$R = 0.02$, $P = 0.001$	$R = 0.14$, $P = 0.001$	
N_X	$R = 0.36$, $P = 0.001$	$R = 0.48$, $P = 0.001$	$R = 0.40$, $P = 0.001$	$R = 0.36$, $P = 0.001$
Spiders				
I2	$R = 0.01$, $P = 0.454$			
I3	$R = 0.02$, $P = 0.202$	$R = 0.02$, $P = 0.158$		
N_M	$R = 0.03$, $P = 0.002$	$R = 0.14$, $P = 0.001$	$R = 0.01$, $P = 0.362$	
N_X	$R = 0.17$, $P = 0.001$	$R = 0.05$, $P = 0.008$	$R = 0.02$, $P = 0.048$	$R = 0.18$, $P = 0.001$
Carabids				
I2	$R = 0.01$, $P = 0.206$			
I3	$R = 0.01$, $P = 0.531$	$R = 0.01$, $P = 0.746$		
N_M	$R = 0.19$, $P = 0.001$	$R = 0.17$, $P = 0.001$	$R = 0.17$, $P = 0.001$	
N_X	$R = 0.49$, $P = 0.001$	$R = 0.57$, $P = 0.001$	$R = 0.48$, $P = 0.001$	$R = 0.64$, $P = 0.001$

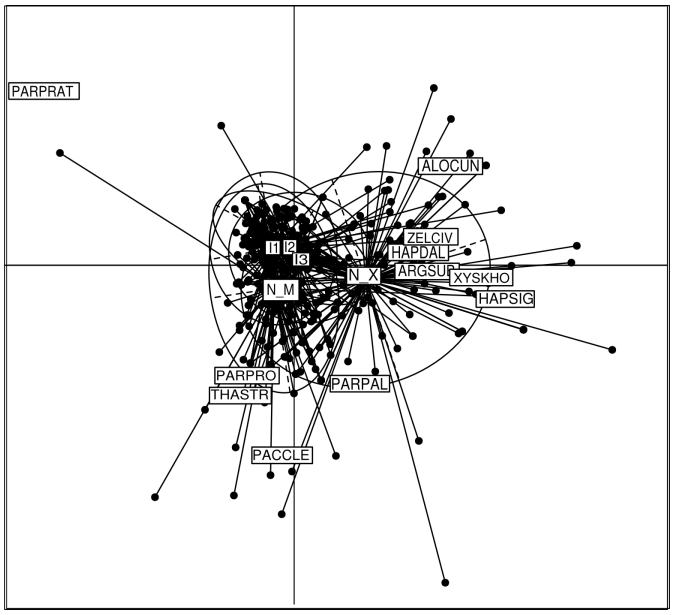

Figure 2.5 – Correspondence Discriminant Analysis of the spider species classified by time class since water withdrawal. Species presented are the ones that contributed most to the axes. Ellipses represent the summarized weighted scatter plot for each class.

Assemblages from habitats 1-9, 10-19 and >20 days after flooding had subsided presented no significantly different species compositions from each other (ANOSIM, Table 2.2). Assem-

blages from habitats 1-9 and 10-19 days after flooding had subsided were characterised by *Pardosa prativaga* (Figure 2.6; confirmed by IndVal=0.77, $P = 0.004$ and IndVal=0.55, $P = 0.01$, respectively). *Ozyptila simplex* was an indicator of stations that had been free from floodwater for more than 20 days (IndVal=0.48, $P = 0.005$). NOn-flooded meso-hygrophilous stations were characterised by the presence of *Pardosa proxima* (confirmed by IndVal=0.31, $P = 0.005$), *Pachygnatha clercki* (confirmed by IndVal=0.22, $P = 0.005$) and *Thanatus striatus* (confirmed by IndVal=0.16, $P = 0.05$), and presented a significantly different species composition from flooded stations (ANOSIM, Table 2.2). Regarding flooding per se, *Pardosa prativa* was an indicator of flooded sites (IndVal=0.77, $P = 0.004$), whereas *Haplodrassus signifer* (IndVal=0.73, $P = 0.002$), *H. dalmatensis* (IndVal=0.64, $P = 0.002$), *Xysticus kochi* (IndVal=0.64, $P = 0.002$), *Zelotes civicus* (IndVal=0.58, $P = 0.004$), *Pelecopsis mengei* (IndVal=0.54, $P = 0.04$), *Argena subnigra* (IndVal=0.45, $P = 0.018$) and *Pachynatha clercki* (IndVal=0.45, $P = 0.036$) were indicators of non-flooded stations.

The two first axes of the CDA on carabids explained 87.4% of the total variance and permutation tests showed that the group discrimination was significant ($P < 0.001$). The assemblage from non-flooded xerophilous stations presented a clearly different species composition (ANOSIM, Table 2.2) and was characterised by *Harpalus dimidiatus*, *H. serripes*, *H. anxius* and *H. latus* (Figure 2.6).

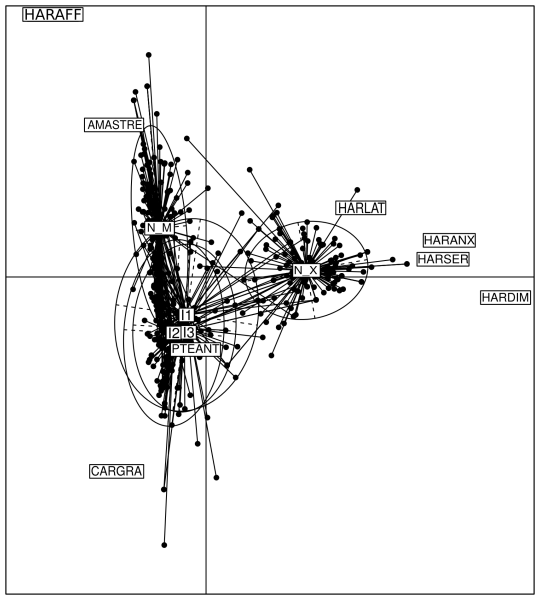

Figure 2.6 – Correspondence Discriminant Analysis of the carabid species classified by time class since water withdrawal. Species presented are the ones that contributed most to the axes. Ellipses represent the summarized weighted scatter plot for each class.

Assemblages from stations free from flood water for 1 to more than 20 days were characterised by *Carabus granulatus* and *Pterostichus anthracinus* and presented no significantly different species compositions (ANOSIM, Table 2.2). Non-flooded meso-hygrophilous stations, characterised by the presence of *H. affinis* (confirmed by IndVal=0.40, $P = 0.015$) and *Amara strenua* presented a significantly different species composition from all other stations (ANOSIM, Table 2.2). Regarding flooding per se, *Carabus granulatus* was an indicator of flooded stations (IndVal=0.59, $P = 0.024$), whereas *Harpalus affinis* (IndVal=0.85, $P = 0.002$), *H. latus* (IndVal=0.84, $P = 0.002$), *H. luteicornis* (IndVal=0.72, $P = 0.002$), *H. serripes* (IndVal=0.68, $P = 0.002$), *Amara strenua* (IndVal=0.67, $P = 0.006$), *H. dimidiatus* (IndVal=0.66, $P = 0.002$), *H. anxius* (IndVal=0.64, $P = 0.002$), *H. rufipes* (IndVal=0.48, $P = 0.024$) and *Amara rufipes* (IndVal=0.48, $P = 0.024$) were indicators of non-flooded stations.
Considering the clear difference in the composition of non-flooded xerophilous stations and other stations (see Figures 2.4, 2.6 and 2.5 and above), non-flooded xerophilous grasslands were removed from further analyses, as they could not be considered as refuges or sources for recolonisation.

Recolonisation process

Activity-density and species richness of spiders varied significantly between flood categories ($\chi^2 = 19.08$, $P < 0.001$ and $\chi^2 = 35.45$, $P < 0.001$, respectively). There was no significant difference between activity-density in the stations 1-9 days after flood withdrawal or in non-flooded meso-hygrophilous stations (Table 2.3 and Figure 2.7). Activity-density was highest for stations free from floodwater for 10 to more than 20 days after water withdrawal. Spider species richness observed for stations free from flood water for 1-9 days was significantly lower than species richness observed for stations non-flooded for 10 to more than 20 days and non-flooded meso-hygrophilous stations (Table 2.3 and Figure 2.7).

Table 2.3 – Mean activity-density (AD± s.d.) and species richness (S± s.d.) of carabids and spiders, with non parametric Kruskal-Wallis tests values followed by two-sample Wilcoxon post-hoc tests between stations, 1–9 days (I1), 10–19 days (I2), more than 20 days (I3) since water withdrawal and non-flooded xerophilous (N_X) and meso-hygrophilous (N_M) grasslands, for all arthropods, spiders and carabids.

	I1	I2	I3	N_M	Test	Post-hoc
Spider AD	1.13 ± 0.85	1.49 ± 0.76	1.29 ± 0.65	1.06 ± 0.73	χ^2 =19.08, $df = 3$, $P < 0.001$	N_M<I3<I2, I1<I2
Spider S	2.16 ± 1.78	3.52 ± 2.13	3.55 ± 1.91	3.02 ± 2.11	χ^2=35.45, $df = 3$, $P < 0.001$	I1<I2=I3=N_M
Carbid AD	0.54 ± 0.53	0.95 ± 0.48	1.10 ± 0.52	1.11 ± 0.52	χ^2=77.88, $df = 3$, $P < 0.001$	I1<I2=I3=N_M
Carabid S	1.76 ± 1.78	3.15 ± 1.61	3.32 ± 1.69	3.95 ± 2.06	χ^2=82.27, $df = 3$, $P < 0.001$	I1=I2=I3<N_M

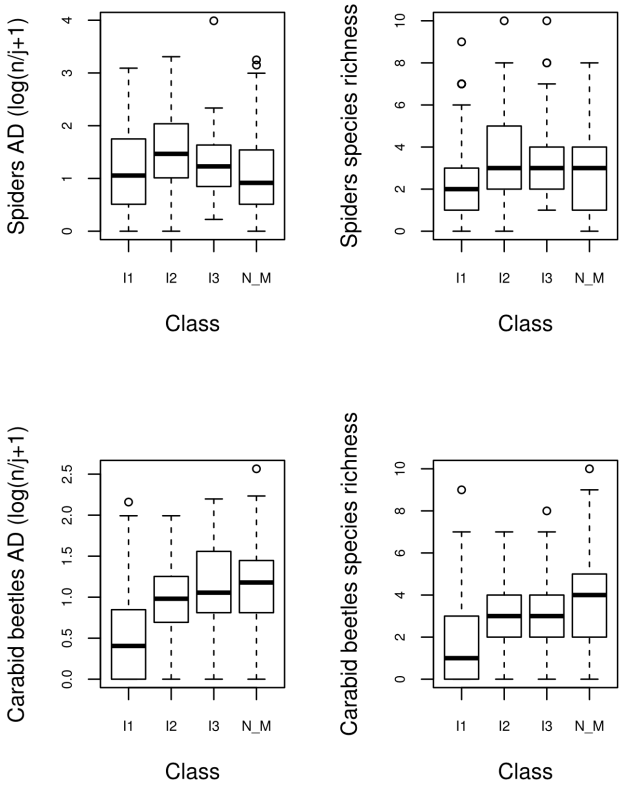

Figure 2.7 – Activity-density (AD) and species richness of spiders and carabids for each time class since water withdrawal (1–9 days (I1), 10–19 days (I2), more than 20 days (I3), non-flooded xerophilous (N_X), non-flooded meso-hygrophilous (N_M)). Box plots represent median, 25 and 75%-quartiles, and max/min values.

Activity-density and species richness of carabids were significantly different between flood categories (respectively $\chi^2 = 77.88$, $P < 0.001$ and $\chi^2 = 82.27$, $P < 0.001$). Activity-density and species richness in stations 1-9 days after water withdrawal were significantly lower than they were in other stations (Table 2.3 and Figure 2.7). Species richness of stations 10 to more than 20 days after floodwater withdrawal was significantly lower than species richness in non-flooded meso-hygrophilous stations (Table 2.3 and Figure 2.7).

Effect of landscape configuration

MANOVAs on spider activity-density for the three size classes showed significant differences between classes of distance to the nearest hedgerow ($F = 6.41$, $P < 0.001$), woodland ($F = 3.90$, $P < 0.001$) and non-flooded meso-hygrophilous grassland ($F = 2.40$, $P = 0.027$). Post-hoc Tukey HSD tests showed different effects of distance to hedgerow on the size classes. Activity-density of medium and large spiders was greater near hedgerows whereas activity-density of small spiders was highest far from hedgerows (Table 2.4). Distance to the nearest woodland also had contrasting effects: activity-density of small spiders was highest far from woodlands whereas activity-density of large spiders was highest near woodlands (Table 2.4). Post-hoc Tuckey HSD tests were not significant for distance to the nearest non-flooded meso-hygrophilous grassland.

Table 2.4 – MANOVA and Tukey HSD post-hoc tests on the functional traits of spiders and carabids. For spiders, size classes are C1: 0–3 mm, C2: 3–5 mm, C3 > 5 mm; for carabids, size classes are C1: 0–5 mm, C2: 5–10 mm, C3 > 10 mm. Distance classes to the nearest hedgerow are: DH1: 0–100 m, DH2: 101–200 m and DH3: > 200 m. Classes to the nearest woodland are DW1: 0–300 m, DW2: 301–600 m and DW3: > 600 m. Distance classes to the nearest non-flooded habitats are DNF1: 0–100 m, DNF2: 101–200 m and DNF3: >200 m.

	Hedgerow	Woodland	Non flooded site	Nearest refuge
Spiders				
Lenght	$F_{2,494}$=6.41, $P < 0.001$	$F_{2,494}$=3.90, $P < 0.001$	$F_{2,494}$=2.40, $P = 0,027$	$F_{2,494}$=1.85, $P = 0.087$
C1	DH1<DH3	DW1=DW2<DW3	n.s.	
C2	DH3<DH2=DH1	n.s.	n.s.	
C3	DH3<DH2<DH1	DW3<DW2	n.s.	
Dispersion	$F_{2,494}$=12.05, $P < 0.001$	$F_{2,494}$=2.55, $P = 0.080$	$F_{2,494}$=8.16, $P < 0.001$	$F_{2,494}$=1.11, $P = 0.33$
Running	DH3<DH2<DH1		DNF3<DNF2<DNF1	
Ballonning	DH1<DH3		n.s.	
Carabids				
Lenght	$F_{2,494}$=9.87, $P < 0.001$	$F_{2,494}$=3.88, $P < 0.001$	$F_{2,494}$=1.63, $P = 0.138$	$F_{2,494}$=0.64, $P = 0.696$
C1	DH1=DH2<DH3	n.s.		
C2	DH2=DH3<DH1	DW1=DW2<DW3		
C3	DH2=DH3<DH1	n.s.		
Wing development	$F_{2,494}$=2.97, $P = 0.019$	$F_{2,494}$=4.87, $P < 0.001$	$F_{2,494}$=2.51, $P = 0.041$	$F_{2,494}$=1.64, $P = 0.162$
Brachypterous	n.s.	n.s.	n.s.	
Macropterous	n.s.	DW1=DW2<DW3	n.s.	

MANOVAs on spider activity-density observed for the dispersal habits showed significant differences between classes of distance to the nearest hedgerow ($F = 12.05$, $P < 0.001$), and to the nearest non-flooded meso-hygrophilous grassland ($F = 2.14$, $P = 0.047$: Table 2.4). Post-hoc Tukey HSD tests showed contrasting effects of distance to hedgerow, with greater activity-density of ground-running spiders near hedgerows whereas activity-density of ballooning spiders was highest far from hedgerows (Table 2.4). Activity-density of ground-running spiders was also greater when distance to the nearest non-flooded meso-hygrophilous grassland decreased (Table 2.4).
MANOVAs on carabid activity-density for the three size classes showed significant differences between classes of distance to the nearest hedgerow ($F = 9.87$, $P < 0.001$) and to the nearest woodland ($F = 2.95$, $P = 0.007$: Table 2.4). Post-hoc Tukey HSD tests showed contrasting effects of distance to hedgerow, with activity-density of medium and large carabids being greater near hedgerows whereas activity-density of small carabids was highest far from hedgerows (Table 2.4). Activity-density of medium carabids was highest far from woodlands (Table 2.4).
MANOVAs on carabid activity-density observed for the two classes of wing development showed significant differences between classes of distance to the nearest hedgerow ($F = 2.97$, $P < 0.019$) and to the nearest woodland ($F = 4.87$, $P < 0.001$) (Table 2.4). Post-hoc Tukey HSD tests showed significant effects of distance to woodlands for macropterous carabids, with activity-density of these species being higher far from woodlands (Table 2.4).

Discussion

Changes in arthropod composition over time

The DCA and ANOSIM on the whole arthropod assemblage demonstrated that flooded sites presented similar compositions over time, suggesting slow resilience of ground arthropod communities to spring floods. A spider family (Lycosidae), with high dispersal abilities, was characteristic of all flooded habitats. The habitats only flooded in winter were characterised by Staphylinidae, Polydesmidae and Formicinae. Staphylinids have been reported to survive 30 days of immersion at low (i.e. winter) temperatures (Adis, & Junk, 2002) and are usually associated with wet habitats (Greenwood et al., 1991). Polydesmidae can be encountered from very dry to very wet habitats (Voigtländer, 2011) but to our knowledge, no study has investigated their resilience after flooding. Ants, and especially the Formicinae sub-family, are known to adapt very well to extreme perturbation including unpredictable flooding (Nielsen, 2011; Lenoir, 2006). In our study, even if ants appear to be characteristic of non-flooded meso-hygrophilous sites, they represent 6% of arthropods collected in the ten first days after the water receded, and 11% of arthropods caught between 10 and 20 days after the water subsided. This suggests that some colonies resisted inundation in their nests (Nielsen, 2011).

Comparison of spider and carabid recolonisation after flooding

In this study, spiders and carabids were the two most highly dominant groups of arthropods, reinforcing the need to focus on their species composition. Species composition of the spider assemblage 20 days after the water had subsided was not different from that observed in non-flooded meso-hygrophilous grasslands, whereas the composition of carabid assemblage dffered until the end of our study. Additionally, species richness of spiders reached the same level as non-flooded meso-hygrophilous grasslands between 10 and 20 days after the floodwater had receded, whereas species richness of carabids did not, even after more than 20 days. This is in accordance with the findings of Gerisch et al. (2012) for carabids after a summer flood, but contrary to numerous studies stating that riparian ground beetles are highly resilient to regular and periodic floods (e.g. Adis, & Junk, 2002; Zulka, 1994; Uetz, 1979; Lessel et al., 2011).

The spider assemblage in flooded habitats was clearly dominated by a ground-dwelling species: *Pardosa prativaga*. This species is associated with open habitats and is considered ubiquitous (Harvey et al., 2002). Like most lycosids, this species has high dispersal abilities; Richter et al. (1971) estimated a mobility of 34.5cm/min, in a straight line, in the field (i.e., around 500 m a day). *Pardosa prativaga* activity-density decreased from 75.8% of total activity-density of spiders in the 10 first days after water withdrawal to 53.7% after 20 days from water withdrawal. This suggests that *P. prativaga* is the first species to recolonise grasslands after floodwater has receded. The species can thus be considered an indicator of flooded habitats, and its presence would indicate ongoing recovery (Gerlach et al., 2013). Non-flooded hygrophilous grasslands are characterised by two hygrophilous species: *Pardosa proxima* and *Pachygnatha clercki* (Harvey et al., 2002), but are numerically dominated by *Pardosa prativaga* (51% of all spiders). Flooded habitats are thus dominated by an opportunistic spider species with a typical "risk strategy" whereas non-flooded meso-hygrophilous grasslands are characterised by stenotopic (hygrophilous) species. This segregation between sites that are flooded only in winter and those flooded in both winter and spring is in accordance with Sudd (1972) and Uetz (1979); both the studies showed that flooding frequency was an easy way to discriminate spider assemblages. However, this is in opposition with the findings of Bell et al. (1999), who showed that spider assemblages are shaped according whether a site is flooded.

Flooded habitats were characterised by two hygrophilous (Desender et al., 2008) carabid species, *Carabus granulatus* and *Pterostichus anthracinus* and numerically dominated by *Poecilus cupreus*. *P. cupreus* is considered eurytopic, with an affinity for wet habitats and with high dispersal abilities (up to 30 m/days in the field: Thiele 1977). Its ability to swim across small water bodies has also been reported (Sienkiewicz, & Zmihorski, 2012).

Non-flooded meso-hygrophilous grasslands are characterised by two carabid species with unclear habitat requirements: *Harpalus affinis* and *Amara strenua*. *H. affinis* is considered an eurytopic species with affinities for dry grasslands by Desender et al. (2008) but Van Looy et al. (2007) found

that this species is a quick coloniser of riparian habitats, although it is also sensitive to rapid flow increases. The rising water observed in 2012 could have been slow enough to allow *H. affinis* to retreat into non-flooded habitats, explaining its dominance in the non-flooded meso-hygrophilous stations (27% of total catches). *Amara strenua* is considered by Luff (1998) as a coastal species that can be found on river banks. Follner, & Henle (2006) consider *A. strenua* a resident of transition zones between dry and wet habitats, which is in accordance with our findings.

The low richness of hydrophilic species in flooded sites is in opposition with Lessel et al. (2011) who found an increased number of hygrophilic species with increasing soil moisture. The long period without spring flood in the Loire valley (8 years) could have allow eurytopic species to colonise grasslands and exclude hygrophilic species.

The non-flooded xerophilous sites were characterised by species of dry habitats: *Harpalus latus*, *H. anxious*, *H. serripes* and *H. dimidiatus* (Desender et al., 2008; Luff, 1998) for carabids and *Xysticus kochi* and *Haplodrassus dalmatensis* for spiders. Therefore, these grasslands cannot be considered refuges. Results of the IndVal approach confirmed the CDA for carabids when looking at flooded site vs non-flooded site indicators but did not function very well when looking for indicators of time class since the water had receded, suggesting that carabids are less resilient than spiders.

The variations in activity-density between the flood categories presented different patterns between spiders and carabids. The activity-density of spiders reached the same level as non-flooded meso-hygrophilous grassland immediately after water receded and was the highest 10–19 days after flooding. The lack of spatial competition after flooding could explain this observation (Hering et al., 2004). Besides, on river banks prey sources of spiders and carabids are known to switch from terrestrial to aquatic after flooding (Paetzold et al., 2005; O'Callaghan et al., 2013). The same behaviour in flooded grasslands could explain the high activity of Lycosidae. Indeed, this behaviour is mainly observed in species with traits that favoured rapid dispersal (O'Callaghan et al., 2013). The fast resilience of spiders compared to carabids has recently been reported after severe disturbance (e.g. Varet et al., 2013b). The dominance of adult lycosids at the beginning of water withdrawal (92.6%) suggests that spiders of this family avoid flooding by actively retreating to refuges or by resisting it. The activity-density is greatest between 10 and 20 days after the water receded, suggesting active colonisation of empty habitats. For carabids, the important difference in activity-density (-49%) between non-flooded habitats and habitats 1 to 10 days after water withdrawal suggests high mortality caused by the flood. Activity-density did not reach the level observed in the non-flooded habitats, even after 30 days after the water receded, suggesting a medium- to long-term resilience of the assemblage. Those findings are in accordance with the results of (Hering et al., 2004), which found carabid density to be the lowest one month after a 100-year flood, and highest two months after the flood. These results are also in accordance with the findings of Rothenbücher, & Schaefer (2006) on strategies used by spiders during winter flooding, but not by carabids. These authors found that leafhoppers and planthoppers could tolerate winter flooding, whereas spiders and carabids emigrate to safe places. Spring flooding could have

occurred faster than winter flooding, allowing spiders, but not most carabids, to emigrate. Gerisch et al. (2012) found that the total species richness of carabids reached a level similar to that of pre-flood condition within 2 years of an extreme summer flood.

Influence of landscape configuration in the recolonisation process

As expected, landscape configuration had an impact on some functional traits of spiders and carabids. Activity-density of medium and large individuals of the two groups was higher near hedgerows and the activity of small species was greater farther from them. Hedgerows could constitute a refuge for medium-sized carabids and large species of spiders with high active dispersal abilities. Such vertical migrations have been reported in ants and millipeds in the Pantanal (Adis et al., 2001). For large carabids, usually considered to have a lower dispersal capacity (Dajoz, 2002), natural hedgerows are frequently used as overwintering sites. Higher activity-density of large carabids species could thus reflect the emergence of adults in early spring. Higher activity-density of small species far from hedgerows could result from a barrier effect of hedgerows on aerial dispersers (Larrivée, & Buddle, 2009). A significant effect of distance to hedgerows was found for the dispersal habits of spiders. As ground runners are usually medium or large species and ballooners are small species, our results are obviously in accordance with those found for the size class analysis. We found no impact of distance to hedgerows on the wing development of carabids. Indeed, only one species (*Carabus granulatus*) was brachypterous, and half of its population was located in a site next to a hedgerow (30m). This suggests that this hygrophilous species, usually associated with grasslands, is also dependent on the presence of hedgerows in flooded sites. However, the species is able to survive for over 10 days above water (Decleer, 2003), which probably explains its presence on the study site.
The influence of distance to woodlands is less clear as it influenced the activity-density of small and large spiders only. This is probably due to the spatial distribution of the two small woodlands that were relatively far from the flooded habitats. Distances to non-flooded meso-hygrophilous grasslands and to the nearest refuge did not affect the functional traits of spiders and carabids, suggesting that these taxa are likely to actively retreat into hedgerows and woodlands, even if there is another, nearer, refuge available. Thus, it seems that never-flooded sites that serve as refuges during winter floods (Andersen, 2011), do not serve as refuge during spring-floods.

In conclusion, we showed that spring-flooded, winter-flooded and never-flooded habitats presented clear, discrete compositions. As expected, spiders and carabids were the most resilient arthropod groups after a severe spring flood, especially Lycosidae and Pterostichini. Spiders almost recovered only 20 days after flooding, suggesting that spring floods are, as expected, less severe than summer floods for this group. Carabids, despite being known to be well adapted to

floodplain ecosystems, appeared less resilient than spiders, confirming the relevance of multi-taxon based studies. Finally, we found that the role of landscape in the recolonisation by spiders depends on their body size and dispersal habits. Recolonisation of carabids was mainly dependent on their size and on the presence of hedgerows. For both spiders and carabids, hedgerows, and to a lesser extent woodland, seem to constitute preferential refuges, which should be considered carefully, as hedgerows are continuously decreasing in agricultural landscapes. The original conclusions drawn here from less studied habitats, flooded meadows, should be tested in other large European streams with few disturbed hydrological functioning.

Impacts de la gestion des prairies de fauches sur les arthropodes épigés

Cette section est présentée sous la forme d'un article publié dans la revue *Agriculture, Ecosystems & Environment*:
Lafage D. & Pétillon, J. (2014). Impact of cutting date on carabids and spiders in a wet meadow. *Agriculture, Ecosystems & Environment*, 185, 1–8.

Figure 3.1 – Ile aux Chevaux (Sainte-Gemmes-sur-Loire): fauche d'une prairie. Juin 2013.

3.1 Résumé

Les araignées et coléoptères carabiques sont connus pour être particulièrement sensibles à la gestion des milieux qu'ils occupent. En tant qu'auxiliaires des cultures maintenant reconnus, ils représentent un compartiment biologique essentiel des milieux agricoles.
Dans la Vallée de la Loire, les prairies semi-naturelles sont essentiellement gérées par la fauche ou le pâturage. De nombreuses études se sont penchées sur les impacts de ces deux modes de gestion sur l'arthropofaune. Cependant, les recherches portant sur l'impact de la date de fauche à court et long terme sont rares et concernent essentiellement les oiseaux et la végétation.
Dans ce chapitre, nous avons étudié l'impact de la date de fauche dans les prairies inondables sur l'activité-densité, la richesse spécifique et les traits fonctionnels des araignées et des coléoptères carabiques.
Au total, 26392 araignées (56 espèces) et 12278 carabiques (82 espèces) ont été capturés et identifiés. Les deux groupes ont fortement été impactés par la fauche en elle-même, aussi bien en termes d'activité-densité que de richesse spécifique ou de traits fonctionnels. L'impact sur les carabiques se situait plus particulièrement à long terme alors qu'il se situait à court terme pour les araignées. Nous n'avons pas mis en lumière d'effet à long terme de la date de fauche. En revanche, à court terme, les effets négatifs sur les araignées, concernant l'activité-densité, la richesse spécifique et les guildes de chasse, décroissent avec le retard de la date de fauche. Les effets sur les carabiques sont peu nombreux et s'accroissent avec le retard de la date de fauche. Ils ne concernent que les traits fonctionnels et plus particulièrement la taille des individus.
Nos résultats suggèrent donc une plus grande sensibilité, à court terme, des araignées et des dates de fauches optimales opposées entre les deux groupes. Cela nous amène à promouvoir la mise en œuvre de politiques permettant de garantir une hétérogénéité spatiale des dates de fauche.

3.2 Impact of cutting date on carabids and spiders in a wet meadow

Abstract

The impact of different cutting dates on two dominant groups of ground-dwelling arthropods (carabids and spiders) was assessed. Short-term impacts were assessed by comparing them before and after cutting.
Arthropods were collected by pitfall traps located in three plots with different cutting dates between June and August and one uncut control plot. Trapping was performed during a 4-month period in the spring and summer 2011. In total, 26,392 spiders and 12,278 carabids, representing 56 and 82 species respectively, were collected. Overall, the effects of cutting were negative and mostly visible in the long term for carabids, with reduced abundances and species richness in cut plots, and in

the short-term for spiders; several parameters (proportion of predators and polyphagous species, and body length) decreased after cutting while remaining stable in the control. Long-term cutting effects revealed almost no differences between plots cut at different dates whereas the short-term effects decreased slightly over time, with respect to the overall phenology of both groups.
In conclusion, this study underlines the fact that cutting has drastic effects on ground-dwelling arthropods, and even late dates, which are supposedly positive for other animals like breeding birds, are deleterious for highly diverse and species-rich grassland groups.

Introduction

Semi-natural grassland is frequently managed to conserve early successional species and assemblages, and to prevent vegetation succession. Cutting is frequently used in habitat conservation to prevent the growth of bushes and trees, and thus maintain semi-natural grassland (Grime, 2001). Its impact on vegetation (e.g. Bakker et al., 2002; Parr, & Way, 1988), birds (e.g. Britschgi et al., 2006) and phytophagous arthropods (e.g. Morris, & Plant, 1983) has been well studied, but has been less well examined regarding predatory arthropods. Cutting is supposed to have a negative effect on invertebrate diversity in general (Ausden, 2007), and on spiders (Bell et al., 2001; Prieto-Benítez, & Méndez, 2011) or leafhoppers (Rothenbücher, & Schaefer, 2006) in particular. Arthropods are however a key component of grassland ecosystems, and particularly spiders and carabids that can play a role in pest control (Symondson et al., 2002).
Spiders are sensitive to changes in habitat structure (Duffey, 1993), particularly those impacting the spatial arrangement of vegetation and litter structures (Uetz, 1991). Baines et al. (1998) reported that, for field margins, the timing of some regimes is more favourable than others: spring and autumn cutting regimes have much less severe effects on the spider community than those with summer cuts, particularly those combined with a spring cut. Purvis, & Curry (1981) also suggested that availability of prey, such as Collembola, may be drastically reduced following cutting, thus affecting specialised spiders.
Carabids are usually considered to be dependent on several abiotic and biotic factors, including (1) temperature or humidity, (2) food conditions, (3) presence and distribution of competitors, and (4) life history and season, including migration between hibernation and reproduction habitats (Lövei, & Sunderland, 1996).
In this study, the impact of different dates of cutting on two dominant groups of ground-dwelling macro-arthropods, ground beetles and spiders, was assessed. Long- and short-term impacts of cutting date were distinguished by comparing assemblages among treatments before/after cutting respectively. More specifically, changes in species richness, total abundance, and traits (niche size, and trophic guild) were investigated by comparing plots differing in cutting dates with a control uncut plot. We hypothesised that cutting per se would have a negative long-term impact on activity-density and species-richness of both groups and would favour generalist species. The

reduction of vegetation complexity and litter-depth could have a negative effect on web-building spiders. Late cutting date induces vegetation modifications by favouring annual plant species (Amiaud et al., 1996). So, we expected cutting date to have a long-term impact on carabids' diet. Short-term impact of cutting per se was expected to be strong especially on activity-density, species-richness and species length. We also expected strong modifications in habitat preferences. Short-term cutting-date impact was expected to be linked to group phenology, early and late cutting having more negative impacts.

Material and methods

The study site was located near the city of Angers, western France (Long: 0 ° 32'37.7" W Lat: 47 ° 30'05.6" N). It was a 600 ha island encircled by two rivers and flooded for about three months each year. The land was mainly covered by hay meadows and a few poplar groves. Grassland were generally cut in summer and grazed by cattle in autumn. Fertilizers have been forbidden for 20 years.

Sampling site

Ground beetles and spiders were sampled in four plots, all being completely covered by meadows. Three plots were under environmental contracts that delayed cutting to a fixed date (E (early): 20/06, M (medium): 10/07, L (late): 20/07) whereas the last one, plot C (control), was not managed except by grazing in autumn. Due to an extremely dry spring followed by a wet summer, farmers had to change the cutting dates in 2011. Early cutting took place on 24th June (instead of the 20th), mid cutting on 28th July (instead of the 10th) and late cutting on 17th August (instead of 20th July). Plots E, M and L belonged to the *Oenanthion fistulosae* (Foucault, 1984) phytosociological association and plot C belonged to the textitBromion racemosi (Tüxen, & Preising, 1951) phytosociological association (see Section 2.3 for description of phytosociological relevés). Management of the four plots has remained unchanged for at least 15 years. Plots E, M and L were separated from each other by small channels (1 m width). Plot E covered 2.9 ha; plot M, 1.4 ha; plot L, 1.9 ha and the control plot covered 0.4 ha. In this study, despite the existence of true replicates within each plot, plots were confounded with the management treatment which can be considered as a case of pseudoreplication in the sense of Hurlbert (1984). Consequently, we increased the spatial sampling effort (Lövei, & Magura, 2011), by placing numerous replicated sampling units per plot.

Sampling was carried out from the 5th May to 31st August 2011, before cattle introduction. Ten traps (100 mm diameter) per plot were set in a square grid. Traps were located at least 25 m from the plot margins and 20 m away from each other to avoid edge effects and interactions between traps (Topping, & Sunderland, 1992). The pitfall traps were filled with preservative

solution (50% monoethylene glycol, 50% water) and emptied every two weeks. In addition, a few days before each cut, all pitfall traps were emptied to prevent destruction and to allow between plot comparisons to be made.

Species identification and functional traits

Carabids and spiders were identified to species level and classified into two classes of habitat preference using Hänggi et al. (1995) and Harvey et al. (2002) for spiders, and Luff (1998) and Bouget (2004) for carabids. Species associated with grassland were classified as specialists and ubiquitous species or stenotopic species not associated specifically with grassland as generalists. Spiders were classified into three guilds (ground runners, ambush hunters, or web-builders) according to their hunting strategy. According to their diet, carabids were classified into three guilds: predators, phytophagous or polyphagous. Length of each species was defined according to Roberts (1995) and Harvey et al. (2002) for spiders and to Luff (1998) and Jeannel (1941) for carabids.

Soil and vegetation characteristics

Soil moisture (M) and temperature (T) were measured on 20th May and 6th June, 2011 using a W.E.T. sensor (5 cm deep) connected to a moisture metre HH2 (both by Delta-T Devices Ltd., Cambridge, UK). Two measurements per sampling point (pitfall trap) were realised and the data were averaged.

Phytosociological observations were carried out on 6th June (i.e. before cutting) using the Braun-Blanquet (1928) approach in a 1 m^2 quadrat around each sampling point. Maximum and average vegetation height and litter depth were measured to the nearest cm. The Normalised Difference Vegetation Index (NDVI), a satellite-derived vegetation index (Tucker, 1979) has been shown to be a useful estimate of productivity and a quantifier of vegetation-related spatial heterogeneity (Levin et al., 2007). NDVI calculation was carried out using Grass GIS software (GRASS Development Team, 2012) applied to a SPOT image (2.5 m resolution, 3 bands) acquired in May 2011 (© CNES (2011), distribution spot image S.A.).

NDVI is defined as:

$$NDVI = \frac{(R_{NIR} - R_{red})}{(R_{NIR} + R_{red})}$$

,

where R_{NIR} and R_{VIS} refer to the reflectance values derived from spectral radiances measured by the near-infrared channel and the visible channel, respectively.

Statistical analysis

Soil and vegetation characteristics were compared between plots using generalised linear models (GLMs) with binomial distribution. When GLM revealed a significant effect of "plot" factor, Tukey's post-hoc tests with Bonferroni correction for multiple comparisons were performed between mean parameters.

Catches in pitfall traps were divided by trapping duration in order to calculate an 'activity density' (the number of individuals per day: Sunderland et al. 1995). To evaluate the impact of cutting date, we studied activity-density ($log(n+1)$ with n as the number of individuals per day), species richness, community weighted mean traits (CWM) (Lavorel et al., 2008) and functional diversity (FD). Functional diversity was computed using Rao's quadratic entropy (BottaDukát, 2005). CWM and FD were computed using FD package (Laliberté, & Legendre, 2010).

To verify independence in the time series before cutting we performed Box-Pierce tests on each plot. The tests demonstrated independence in the time series for all plots, for both carabids (plot E: $\chi^2 = 0.60$, $P = 0.438$; plot M: $\chi^2 = 0.20$, $P = 0.653$; plot L: $\chi^2 = 0.99$, $P = 0.318$; plot C: $\chi^2 = 0.96$,$P = 0.326$) and spiders (plot E: $\chi^2 = 0.95$, $P = 0.331$; plot M: $\chi^2 = 0.01$,$P = 0.968$; plot L: $\chi^2 = 0.98$, $P = 0.322$; plot C: $\chi^2 = 7e^{04}$, $P = 0.980$); so data were not pooled.

In order to test for differences in species richness and activity-density (total and per ecological trait) between the four plots (i.e. the long-term impact of cutting), GLMs with quasi-Poisson distribution were performed using data from the individual traps (Vincent, & Haworth, 1983; O'Hara, & Kotze, 2010) before the first cut took place. When GLM revealed a significant effect of 'plot' factor, Tukey's post hoc tests with Bonferroni correction for multiple comparisons were performed between mean parameters.
As the same trap was operative before and after cutting, abundances were pair-matched over time and consequently compared using repeated analysis of variance (R-ANOVA); see Pétillon et al. (2010) for such statistical treatments and analyses of catches by traps over time. Three trapping series, before and after cutting, were used for early and medium cuts and two were used for the late one (due to cattle introduction). In the case of a significant cutting effect, the interaction between within-subject factor and the fixed factor 'management' was expected to be significant.

Tests were performed for both spiders and carabids using total activity-density, species richness and traits as dependent variables, management (cut or uncut: each cut plot was compared with the uncut control) as a fixed factor, and period (pre- vs. post-cutting) as a within subject effect. If the interaction between fixed factors was not significant (in model 1), a second GLM (model 2) was used to test significant effects of separated fixed factors, without their interaction. If the interaction

was significant, t-tests were used to detect significant differences between sampling periods (i.e. differences between plots which were independent from periods were not of interest here). In the case of short-term cutting effects, a significant interaction between management and period was indeed expected (i.e. the within subject factor being expressed differentially for the two plots due to cutting effects in one of them). For each analysis, the level of statistical significance used was $\alpha = 0.05$. Results were expressed as mean ± S.E. Prior to analysis, normality and homogeneity of variances were checked by Shapiro–Wilk tests and Levene tests respectively, and data were $log(x + 1)$ transformed; sphericity assumption was tested by Mauchly's test before applying R-ANOVAs. All statistical analyses were performed using the R software (R Development Core team, 2013). The Levene tests were performed using the Lawstat package (Noguchi et al., 2012). Post hoc tests were performed using the Asbio package (Aho, 2012).

Results

The control plot differed clearly from the cut plots, as it presented greater litter-depth and NDVI, and had lower number of plant species and soil temperature (Table 3.1). Cutting generally removed all litter and induced lower plant species richness and biomass. No constant differences were found among cut plots: plot M was significantly different from plot E for maximum height of vegetation and moisture. All plots differed significantly regarding soil temperature. A total of 26,392 spiders, of 56 species representing nine families, were trapped. Lycosidae were highly dominant (79.6% of individuals) followed by Linyphiidae (8.2%) and Thomisidae (7.4%). One species accounted for almost 60% of adult individuals: *Pardosa prativaga*. A total of 12,278 adult carabids, belonging to 82 species and 12 tribes, were collected. Two species (*Harpalus rufipes* and *Poecilus cupreus*) accounted for more than 57% of individuals.

Table 3.1 – Means ± S.E. of environmental variables for each plot with GLM results and post-hoc tests. Temperature is given in °C. NDVI = normalised difference vegetation index.

	Plots				GLM		
	E	M	L	C	F	P	Post-hoc
Litter depth	0.53 ± 0.17	0.43 ± 0.25	0.94 ± 0.37	1.47 ± 0.63	13.13	< 0.001	M=E=L<C
Average height	58.75 ± 11.26	38.5 ± 24.73	53 ± 18.74	59 ± 15.78	2.58	0.069	-
Maximum height	92.5 ± 12.81	76.5 ± 27.69	117 ± 23.59	117 ± 22.14	7.59	< 0.001	M<E=L=C
Nb plant species	8.5 ± 1.77	7 ± 1.25	8.3 ± 1.25	5.2 ± 2.53	7.08	< 0.001	E=M=L E=L<C
Moisture	27.05 ± 3.63	23.17 ± 3.33	24.28 ± 2.53	23.71 ± 2.74	2.72	0.06	
Temperature	23.82 ± 0.76	22.68 ± 0.39	21.76 ± 0.53	22.34 ± 0.36	24.71	< 0.001	E>M>L E>C
NDVI	0.18 ± 0.01	0.20 ± 0.01	0.18 ± 0.01	0.22 ± 0.01	21.31	< 0.001	E<M=L<C

Long-term impact of cutting date

There was no significant difference among plots for both activity-density and species richness of spiders (Table 3.2). In contrast, activity-density and species richness of carabids were significantly higher in the control (C) than in the cut plots (Table 3.2) with no difference between the cut plots. A significant long-term impact of cutting date was found on the hunting guild of spiders with more ambush hunters in plot M than in plots L and C, and less ground runners in plot M than in plot L (Figure 3.2). Those differences in CWM trait values were not retrieved in functional diversity of spiders' hunting guilds.

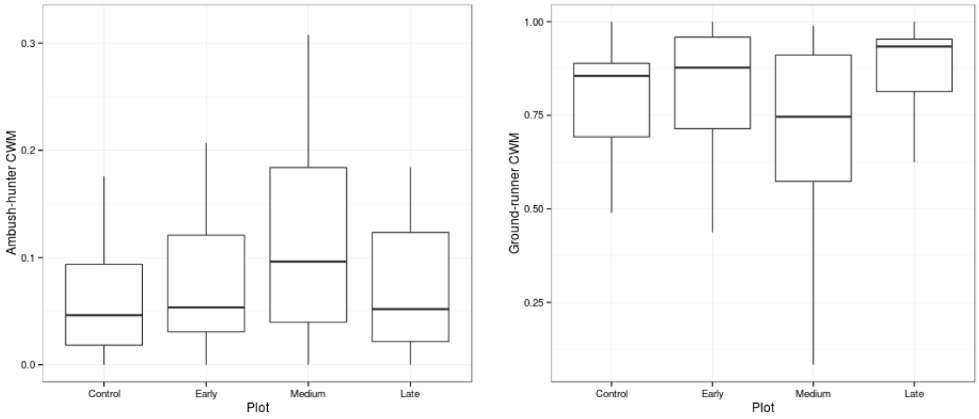

Figure 3.2 – Boxplots of ambush hunters and ground-runners community weighted means (CWM) for each plot. The horizontal bar in the boxplot indicates the median, the ends of the boxes indicate the interquartile range, and the whiskers indicate the 10th and 90th quartiles.

Significant differences were found for carabid diet (Table 3.2). Indeed the control plot had fewer phytophagous than plot L and more polyphagous species than plot M (Figure 3.3). Carabids were also larger in the control plot (Figure 3.3). These differences were retrieved for carabid total FD and diet FD, the control plot presenting smaller values than plots M and L.

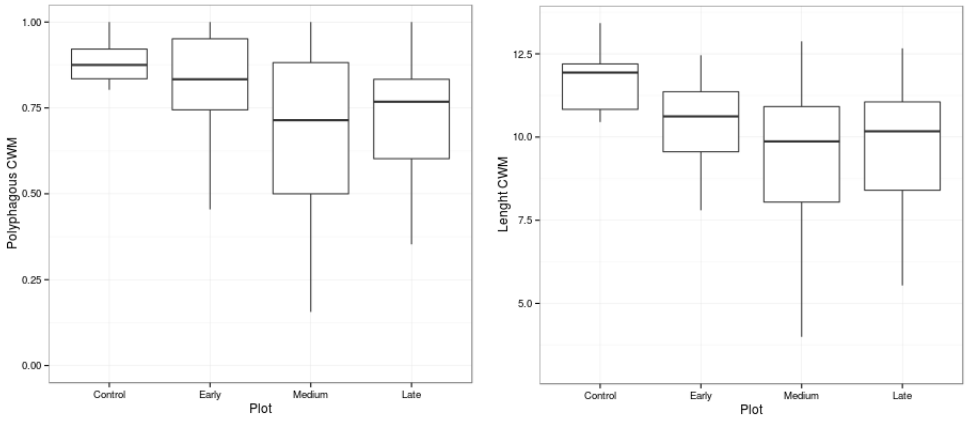

Figure 3.3 – Boxplots of polyphagous and length of carabid community weighted mean (CWM) for each plot. See Figure 3.2 for description.

Table 3.2 – ANOVA (and post-hoc test) of management effect on spiders and carabid beetles activity-density, species richness, functional diversity (FD) and constrained weighted means (CWM) of traits. C = control plot, E = early cut plot, M = medium cut plot, L = late cut plot.

Spiders	(M)ANOVA	Post-Hoc	Carabids	(M)ANOVA	Post-Hoc
Activity density	$F = 3.08$; $P = 0.033$	E=M=L=C	Activity density	$F = 9.66$; $P = 0.033$	C>E=M=L
Species richness	$F = 0.87$; $P = 0.456$		Species richness	$F = 9.69$;$P < 0.001$	C>E=M=L
FD			**FD**		
All	$F = 2.16$; $P = 0,092$		All	$F = 5.86$; $P < 0.001$	C<M=L
Biotop	$F = 1.49$; $P = 0.221$		Biotop	$F = 2.28$; $P = 0.085$	
Guild	$F = 2.26$; $P = 0.085$		Diet	$F = 4.17$; $P = 0.007$	C<M=L
Lenght	$F = 0.48$; $P = 0.698$		Lenght	$F = 1.27$; $P = 0.290$	
CWM			**CWM**		
Habitat	$F = 1.96$; $P = 0.072$			$F = 1.903$; $P = 0.133$	
Generalist	-		Generalist	-	
Specialist	-		Specialist	-	
Guild	$F = 2.19$; $P = 0.008$		Diet	$F = 3.15$; $P = 0.001$	
Ambush hunter	$F = 4.13$; $P = 0.008$	M>L=C	Phytophagous	$F = 4.48$; $P = 0.005$	C<L
Ground runner	$F = 3.01$; $P = 0.030$	M<L	Polyphagous	$F = 4.66$; $P < 0.001$	C=E>M
Web-builder	$F = 2.32$; $P = 0.079$		Predator	$F = 1.46$; $P = 0.229$	
Lenght	$F = 2.53$; $P = 0.060$		Lenght	$F = 4.29$; $P = 0.003$	C>M=L

Short-term impact of cutting date

Overall, most significant effects were found for the period factor, with significant effects decreasing over time. Plot factor was mostly significant for carabids. The interaction between period and plot factors was significant only nine times out of 36 for carabids and eight times out of 36 for spiders, indicating few short-term effects of cutting period (Table 3.3).

Spiders

For the early cutting date, a significant interaction between 'management' and 'period' effects was found for total activity/density. Total activity-density decreased after cutting ($t = 5.54$, $df = 9$, $P < 0.001$) in the early cut plot, whereas activity-density did not change in the control ($t = 1.70$, $df = 9$, $P = 0.123$) (Figure 3.4).

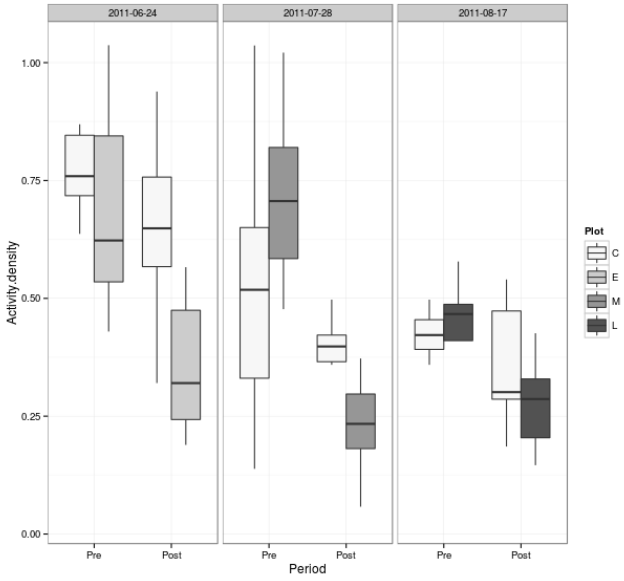

Figure 3.4 – Boxplot of spiders activity-density before (pre) and after (post) cutting for each cutting date. The horizontal bar in the boxplot indicates the median, the ends of the boxes indicate the interquartile range, and the whiskers indicate the 10 and 90th quantiles. C = control plot, E = early cut plot, M = medium cut plot, L = late cut plot.

Table 3.3 – Repeated Analysis of Variance of the effects of plot type and trapping period, and their interaction on carabid and spider activity-density, species richness and community weighted mean (CWM) and functional diversity (FD) values for traits. If interaction is not significant, F and P values presented for period and plot are those from a second model without interaction. AD: Activity-density, S: Species richness, Poly: Polyphagous, Phyto: Phytophagous, AH: Ambush hunter, GR: Ground runner.

		24/06/11						28/07/11						17/08/11					
		Period		Plot		Interaction		Period		Plot		Interaction		Period		Plot		Interaction	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Carabid	AD	27.95	<0.001	33.104	<0.001	2.08	0.17	1.70	0.20	13.20	<0.001	0.78	0.39	2.40	0.13	12.96	0.001	1.08	0.320
	S	3.54	0.068	1.81	0.19	3.72	0.07	0.66	0.42	11.25	0.00	0.71	0.41	0.28	0.60	14.12	<0.001	0.11	0.740
CWM	Length	11.79	0.002	3.80	0.067	16.99	<0.001	0.06	0.803	7.79	0.008	2.97	0.590	3.39	0.089	10.88	0.006	8.26	0.013
	Specialists	0.17	0.680	4.28	0.046	1.26	0.277	25.32	<0.001	8.99	0.005	2.37	0.141	1.09	0.307	0.31	0.581	0.43	0.524
	Generalists	0.17	0.680	4.28	0.046	1.26	0.277	25.32	<0.001	8.99	0.005	2.37	0.141	1.09	0.307	0.31	0.581	0.43	0.524
	Phyto	0.001	0.97	5.17	0.029	0.80	0.384	2.49	0.123	0.00	0.994	0.07	0.800	0.161	0.692	1.24	0.276	0.09	0.764
	Poly	4.91	0.032	6.49	0.015	0.80	0.383	0.31	0.582	0.68	0.415	3.23	0.090	7.10	0.020	0.42	0.526	7.82	0.015
	Predator	0.94	0.346	0.72	0.408	8.67	0.008	1.90	0.185	1.07	0.314	4.74	0.043	7.00	0.020	0.26	0.622	6.05	0.029
FD	All traits	4.54	0.040	8.81	0.005	0.01	0.972	5.87	0.021	4.43	0.042	1.28	0.272	5.86	0.031	0.66	0.432	7.79	0.015
	Length	4.92	0.033	5.55	0.024	1.40	0.252	0.01	0.945	7.65	<0.001	1.66	0.213	0.01	0.002	2.24	0.158	16.94	0.001
	Habitat	0.01	0.941	0.58	0.452	0.54	0.471	9.64	0.004	7.99	0.008	1.09	0.309	0.02	0.898	2.89	0.101	0.01	0.980
	Diet	4.96	0.032	5.41	0.026	0.21	0.651	0.04	0.849	4.49	0.041	0.12	0.737	14.02	0.002	0.78	0.393	14.56	0.002
Spider	AD	25.59	<0.001	10.095	0.005	6.775	<0.001	33.351	<0.001	0.135	0.717	8.129	0.011	5.331	0.028	0.9533	0.337	0.588	0.456
	S	34.224	<0.001	0.0002	0.9887	1.77	0.200	9.553	<0.001	5.962	0.025	10.458	0.004	1.446	0.239	0.008	0.931	1.526	0.237
CWM	Length	37.01	<0.001	44.62	<0.001	14.43	0.001	0.88	0.354	130.68	<0.001	2.19	0.158	0.57	0.457	58.07	<0.001	0.28	0.608
	Specialists	63.29	<0.001	33.32	<0.001	14.41	0.001	0.70	0.407	8.30	0.007	2.72	0.117	2.35	0.137	21.76	<0.001	3.67	0.076
	Generalists	63.59	<0.001	33.11	<0.001	14.52	0.001	0.68	0.415	8.25	0.006	2.67	0.120	2.26	0.144	21.45	<0.001	0.27	0.073
	Web-builder	57.05	<0.001	36.39	<0.001	8.03	0.011	9.21	0.005	77.37	<0.001	0.45	0.512	1.43	0.242	34.55	<0.001	1.95	0.185
	AHr	19.51	<0.001	6.35	0.021	7.71	0.012	2.58	0.117	1.23	0.274	2.01	0.174	1.53	0.226	5.04	0.033	1.03	0.327
	GRr	91.23	<0.001	6.11	0.018	0.34	0.570	6.38	0.016	45.48	<0.001	0.16	0.694	0.05	0.827	9.79	0.004	0.00	0.951
FD	All traits	73.73	<0.001	24.24	<0.001	0.02	0.893	1.52	0.226	8.17	0.007	2.61	0.124	2.11	0.157	6.26	0.018	0.21	0.654
	Length	73.58	<0.001	0.16	0.695	3.08	0.096	4.71	0.037	2.45	0.126	0.39	0.542	0.62	0.438	0.30	0.589	0.09	0.767
	Habitat	56.30	<0.001	5.76	0.022	0.01	0.928	7.78	0.008	0.71	0.406	0.00	0.987	2.38	0.134	1.15	0.293	0.01	0.924
	Guild	64.45	<0.001	0.96	0.335	2.39	0.140	1.75	0.194	0.20	0.655	2.77	0.114	0.83	0.370	0.14	0.709	0.02	0.906

Significant interactions were found for several CWM trait values: web-builders and ambush-hunters CWM, specialist and generalist CWM and length CWM (Table 3.3). The interaction found for web-builders was due to an increase in this guild in the control plot ($t = 9.04$, $df = 13.64$, $P < 0.001$) (Figure 3.5).

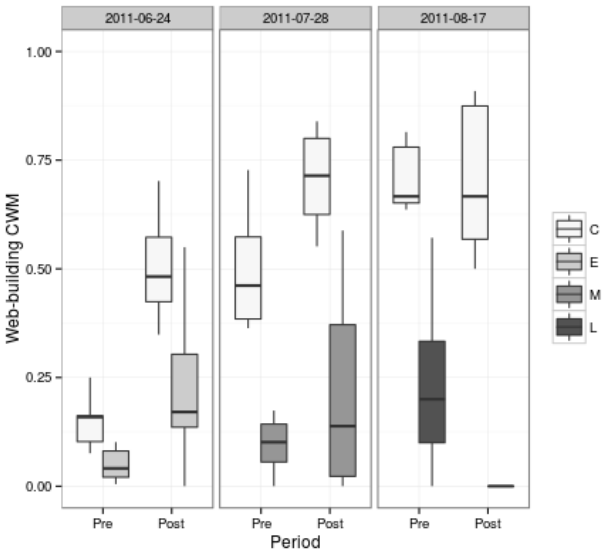

Figure 3.5 – Boxplot of web-builders community weighted means (CWM) before (pre) and after (post) cutting for each cutting date. See 3.4 for description.

The interaction found for ambush-hunters was due to an increase in this guild in the cut plot ($t = 3.35$, $df = 1.14$, $P = 0.006$) whereas it remained stable in the cut plot ($t = 0.02$, $df = 11.35$, $P = 0.984$). The interactions found for specialists and generalists were due to an increase in generalists (plot E: $t = 2.66$, $df = 9$, $P = 0.026$; plot C: $t = 8.98$, $df = 12.19$, $P < 0.001$) and a decrease in specialists in the two plots (plot E: $t = 2.66$, $df = 9$, $P = 0.026$, plot C: $t = 8.97$, $df = 12.18$, $P < 0.001$), changes being greater in the control plot. A significant decrease in spider length was also detected in the control plot ($t = 10.85$, $df = 9$, $P < 0.001$) while it remained stable in the cut plot ($t = 1.28$, $df = 9$, $P = 0.232$). No significant interaction was found for spiders functional diversity.

For the medium cutting date, a significant interaction was found between "management" and "period" effects for total activity-density and species richness of spiders (Table 3.3). Activity-density ($t = 1.91$, $df = 9$, $P = 0.089$) and species richness ($t = 0.17$, $df = 9$, $P = 0.872$) remained stable in the control plot whereas cutting led to a significant decrease in these variables (respectively: $t = 6.72$, $df = 9$, $P < 0.001$ and $t = 4.92$, $df = 9$, $P < 0.001$) in the cut site (Figures 3.4 and 3.6).

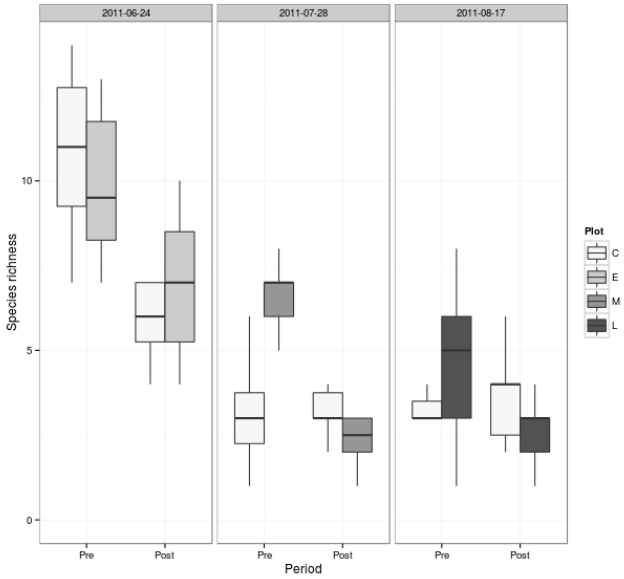

Figure 3.6 – Boxplot of spiders species richness before (pre) and after (post) cutting for each cutting date. See Figure 3.4 for boxplot and abbreviations meaning.

The impact on total activity-density was slightly lower than that observed for early cutting; the differences of estimated average being -0.747 and -0.102 respectively. No significant interaction was found for spider CWM traits values or functional diversity. For the late cutting date, no interaction was found, whatever the variable tested for spiders (Table 3.3).

Carabids

For the early cutting-date, no significant interaction was found for activity-density or species richness (Table 3.3). We found significant interactions for predators and length CWM values. Predators decreased in the control plot ($t = 3.95$, $df = 15.24$, $P = 0.001$) while they remained stable in the cut plot ($t = 1.40$, $df = 14.97$, $P = 0.180$) (Figure 3.7). Length increased in the cut plot ($t = 4.95$, $df = 18$, $P < 0.001$) while it remained stable in the control plot ($t = 0.36$, $df = 17$, $P = 0.720$) (Figure 3.8).

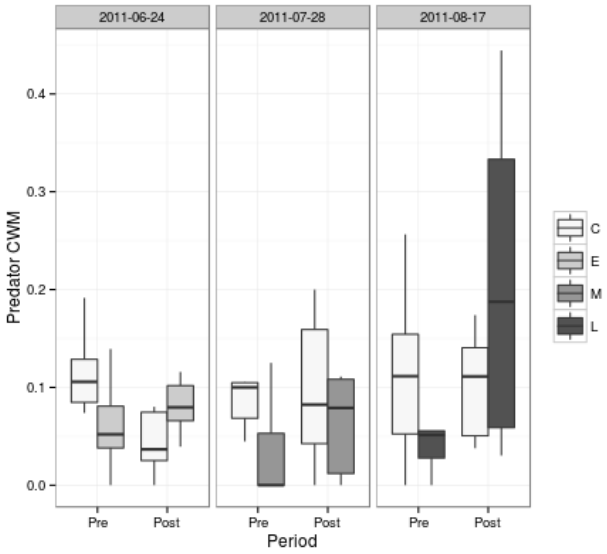

Figure 3.7 – Boxplot of predators community weighted means (CWM) before (pre) and after (post) cutting for each cutting date. See Figure 3.4 for boxplot and abbreviations meaning.

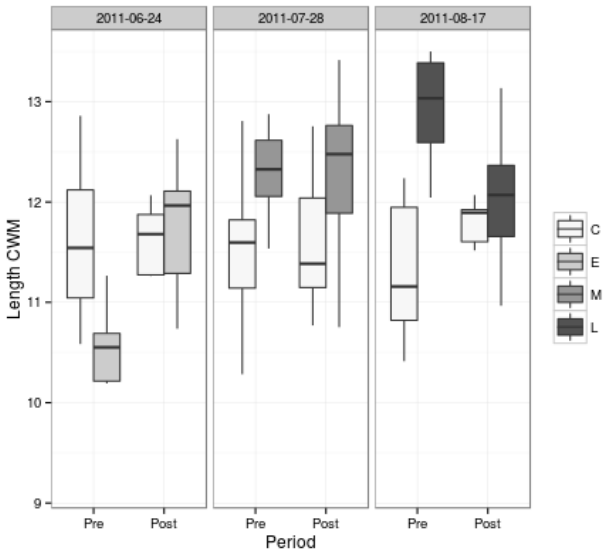

Figure 3.8 – Boxplot of carabids' community weighted means (CWM) length before (pre) and after (post) cutting for each cutting date. See Figure 3.4 for boxplot and abbreviations meaning.

For the medium cutting-date, no significant interaction was found for activity-density and species-richness. A significant one was found for predator CWM, but variations before/after cutting were not significant (control plot: $t = 1.82$, $df = 11.43$, $P = 0.10$; cut plot (M): $t = 0.47$, $df = 17.63$, $P = 0.64$).

For the late cutting-date, no significant interaction was found for activity-density and species-richness, but significant interactions were found for several CWM trait values. The length of carabids decreased significantly in the cut plot ($t = 2.72$, $df = 12.37$, $P = 0.018$) but did not change in the control plot ($t = 1.10$, $df = 8$, $P = 0.305$). Polyphagous decreased significantly in the cut plot ($t = 2.73$, $df = 10.36$, $P = 0.021$) while remaining stable in the control plot ($t = 0.46$, $df = 8.16$, $P = 0.657$) (Figure 3.9). Predators increased significantly in the cut plot ($t = 2.63$, $df = 10$, $P = 0.025$) while remaining stable in the control plot ($t = 0.25$, $df = 8.41$, $P = 0.809$) (Figure 3.7). Significant interactions were found for total, length and diet FD but all the variations were not significant: Total FD: control plot: $t = 1.19$, $df = 15.88$, $P = 0.250$; cut plot (L): $t = 0.53$, $df = 8.42$, $P = 0.608$; length FD: control plot: $t = 1.37$, $df = 7.96$, $P = 0.189$; cut plot (L): $t = 0.40$, $df = 15.91$, $P = 0.703$; diet FD: control plot: $t = 2.01$, $df = 8.36$, $P = 0.063$; cut plot (L): $t = 0.44$, $df = 15.57$, $P = 0.673$.

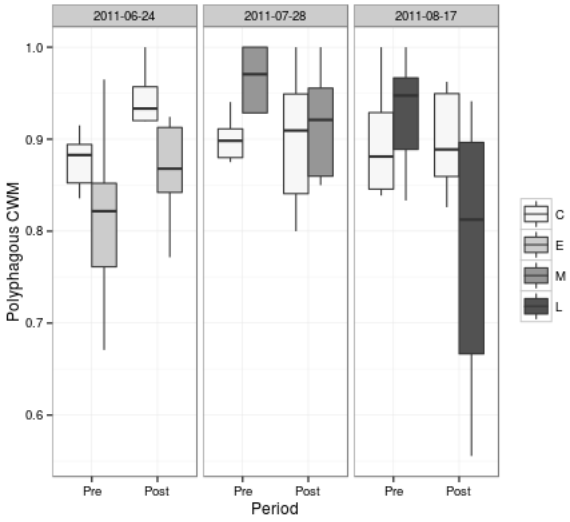

Figure 3.9 – Boxplot of polyphagous community weighted means (CWM) before (pre) and after (post) cutting for each cutting date. See Figure 3.4 for boxplot and abbreviations meaning.

Discussion

In our study, the unmanaged plot supported larger and more diversified carabid beetle communities. These results are consistent with those obtained during the second (short-term) analysis, because the difference between cut and control plots was revealed by the numerous significant effects of the management factor for carabids. This is consistent with the general assumption that management practices, and increased disturbance, decrease the numbers of species and individual carabids (Rushton et al., 1989; Blake et al., 1996; Kotze, & Samways, 1999). Another explanation is given by the higher productivity and complexity of the control plot, as revealed by its NDVI value. This vegetation index is known to be a good predictor of carabid beetle species richness and activity-density (Australian forests: Lassau, & Hochuli 2008, French meadows: Lafage et al. 2014b). In contrast, cutting is reported to have few effects, or if any they are positive, on species richness of both spiders and carabids in salt marshes (Pétillon et al., 2005; Pétillon et al., 2007).
The plot with the medium cutting date presented a higher proportion of ambush hunters which mechanically led to smaller proportion of ground runners. Ambush hunters were mainly represented by *Ozyptila simplex* (87.7% of ambush hunter individuals). Cutting-date had no impact on carabid traits, but cutting per-se affected both diet and length. The fact that carabids of the control plot presented greater lengths, has to be linked to the two dominant polyphagous species present in this plot: *Harpalus affinis* and *H. griseus*. This resulted in a smaller functional diversity of carabid diet in the control plot.

Short-term effects of cutting decreased over time, which is consistent with the phenology of the groups studied. Most species collected were spring breeders, with decreasing activity from June, and a second peak in autumn (for spiders, see Aitchison 1984; for carabids, see Lövei, & Sunderland 1996 and Kotze et al. 2011).
A decrease in the activity-density of spiders was found in the early-cut plot, together with a stronger increase in the proportion of web-builders in the control plot. The numerous impacts on spiders' functional traits were linked to the occurrence of *Pelecopsis mengei* which accounted for more than 80% of Linyphiidae, and was trapped nearly exclusively in the control plot (>95% of all individuals).
Cutting at the end of July had most impact on spiders and affected total activity-density and species richness but not functional traits. Spiders were not impacted at all by late cutting.
Short term effect of cutting was less important on carabids. For the early cutting date, a significant interaction was found for predatory carabids, but it was due to the decrease of this group in the control plot. This weak influence of regime variations is in accordance with Haysom et al. (2004) who found that carabid responses to the three headland cutting regimes took the form of changes in the relative abundance-activity of individual species rather than presence or absence from particular regimes. The impact of medium cutting date was negligible and that of late cut-

ting weak, with a decrease in large and polyphagous carabids in the cut plot, but this may have important implications for conservation. Indeed, very large carabid species, and species associated with both very wet and very dry habitats are considered as conservation priorities (Kotze et al., 2011; Brooks et al., 2012). These results are consistent with the findings of Cole et al. (2005) for carabids, but not for spiders. Cole et al. (2005) found that extensively managed land had a higher relative abundance of large ground beetle (genus *Carabus*) and wolf spider (family Lycosidae) species. Large species tend to have long life-cycles and consequently require a degree of resource stability over time (Blake et al., 1994). Carabids with low dispersal abilities are also known to react more to disturbances than other, smaller, more mobile species (e.g. in agricultural fields and grassland: Hendrickx et al., 2009; Wamser et al., 2012). A significant interaction was found for predatory carabids but it was due to an increase of this group in the cut plot. The open vegetation resulting from cutting might facilitate prey capture for predators resulting in an increase of the group ('hunting efficiency hypothesis').

Overall, cutting had different short-term effects on both groups, with more short-term impacts on spiders. Spiders are well known for their ability to react quickly to some changes in vegetation structure (e.g. Duffey, 1993). Cole et al. (2005) found that, despite an observed relationship between spider and ground beetle assemblages, the highest number of carabid species occurred in intensively managed grassland and arable sites, while the highest number of spider species occurred in semi-natural grassland and heather sites. Spiders high dispersal tendency over both short and long distances (Bell et al., 2005), could explain the differences in their response times (e.g. Varet et al., 2013a) who also found a similar difference in response time between carabids and spiders).

Our results suggest a higher sensitivity of spiders to short-term management effects. In accordance with Bell et al. (2001), we suggest that it would be beneficial to avoid summer cuts where possible and to keep the intensity of cutting as low as possible. As it seems that no ideal cutting-date exists if a multi-taxa conservation approach is performed, we suggest that heterogeneous cutting-dates at local to landscape scales should be promoted to diversify mowing regimes, as indicated by Cizek et al. (2012).

Deuxième partie

Structuration des assemblages d'araignées, de carabiques et de plantes à large échelle

Les habitats des prairies de fauche de la vallée de la Loire: déterminants et cartographie large échelle

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Ce chapitre est présenté sous la forme d'un article en révision majeure dans la revue *Applied Vegetation Science* :
Lafage D., Bonis A., Rapinel S., Ménanteau L. and Bouzillé J-B. Using remote sensing and phyto-sociological approach to assess meadows conservation status. *Applied Vegetation Science*, révision majeure.

Figure 4.1 – Prairie Bruneau. Variations de la physionomie des prairies avec la micro-topographie. Juin 2012.

4.1 Résumé

Les araignées et coléoptères carabiques sont deux groupes connus pour être particulièrement sensibles aux facteurs environnementaux et notamment à la structure de végétation, à l'épaisseur de litière et à l'humidité du sol. Nous avons vu dans la première partie que ces deux groupes étaient également sensibles à la quantité de biomasse végétale, à l'inondation et à la gestion. La végétation est un compartiment intégrateur aussi bien de l'environnement abiotique, des perturbations que de la gestion. Ainsi, être en mesure de cartographier à large échelle les différents habitats prairiaux devrait permettre de disposer d'un couche environnementale essentielle à la compréhension de l'organisation spatiale des peuplements d'araignées et de carabiques.

Dans ce chapitre, nous avons étudié les assemblages de plantes par la méthode phytosociologique. La caractérisation de ces assemblages permet en effet d'approcher l'influence des facteurs environnementaux et des modes de gestion. Pour cela, 578 relevés phytosociologiques ont été réalisés sur l'ensemble de la Vallée de la Loire et des Basses Vallées Angevines en Pays de la Loire ainsi que sur la Basse Vallée de la Vienne.

Les groupements végétaux mis en évidence étaient pour la plupart fortement liés au régime d'inondation et donc à la micro-topographie. Cependant, nous avons aussi mis en évidence l'existence de variantes d'associations liées au type de gestion (en particulier, l'absence de pâturage de regain).

La cartographie végétation est généralement réalisée par photo-interprétation de photographies aériennes. Il s'agit d'une technique très chronophage nécessitant de nombreux relevés de terrain et ne permettant pas de cartographier de grandes surfaces. La cartographie basée sur le traitement d'images satellites permet de contourner ces écueils. Nous avons ici mis en œuvre une cartographie par classification supervisée orientée pixels (par opposition à la cartographie orientée objet) afin de cartographier les associations végétales (au sens phytosociologique) présentes dans la Vallée de la Loire. Cette méthode s'est révélée particulièrement pertinente puisqu'elle atteint une efficacité de classement de 85% y compris pour des variantes d'associations.

Nous nous sommes enfin attachés à explorer le potentiel des cartographies produites en terme d'évaluation de l'état de conservation des habitats.

4.2 Using remote sensing and phytosociological approach to assess meadows conservation status

Abstract

Questions

How wet grassland plant associations and their variations may be mapped using multispectral SPOT-5 images? Does the level of vegetation heterogeneity, estimated from vegetation map produced by supervised classification, provide a reliable prediction of vegetation α-diversity? Does mapping between-year variation in vegetation heterogeneity and/or associations identified as α-diversity loss indicators, allow to detect zones undergoing important α-diversity changes?

Location

Marais d'Audubon, Saint-Étienne-de-Montluc, France.

Methods

Plant associations were mapped using a per-pixel supervised classification with minimum distance classifier on two SPOT-5 images acquired in 2011 and 2012. Correlation between the heterogeneity index applied to habitat maps and plant α-diversity was tested at various scales. Heterogeneity index variations between 2011 and 2012 were studied in situations where an association of low α-diversity was expanding.

Results

Plant associations, as well as their variations, were mapped with a remarkable accuracy (Kappa Index = 0.83). Some variations, in particular those dominated by *Elytrigia repens*, were identified as low α-diversity indicators. Regardless of the spatial scale, we did not find any significant correlation between the vegetation heterogeneity and vegetation α-diversity. Nevertheless, we showed that any variation in the vegetation heterogeneity, either an increase or a decrease, may indicate where there is a substantial risk of α-diversity loss.

Conclusions

Our approach combining a supervised classification on spectral data with phytosociological relevés benefits from the facilities of SPOT-5 images while producing results with good match with the Natura 2000 habitat references. The heterogeneity index appeared to be a poor predictor of plant α-diversity in grasslands while the results obtained suggested that monitoring the variation in vegetation heterogeneity along years could be used to locate vegetation α-diversity important variations. The ability to detect the expansion of the poorly diverse *E. repens* variations at the expense of more diversified associations provides a reliable indicator of a α-diversity loss at the landscape level.

Introduction

Biodiversity conservation is one of the major current concerns in ecosystem management. A correct assessment of the species and habitat conservation status is definitely needed both at the local and landscape scale before any action can be considered by managers. Proposing reliable methodological framework for the evaluation of both the quality and the diversity of natural and semi-natural habitats is thus essential.

A predominant framework for considering the habitat conservation status was provided by the 'Habitats Directive', approved in 1992 by the European Union (EU). This framework lists and describes rare and/or endangered habitats and species requiring conservation action. The habitats in focus thus must be adequately identified and monitored along space and time (Nagendra, 2002). In the Habitat Directive, habitats are classified according to the phytosociological system (Braun-Blanquet, 1928), a method that is still up to date for investigating floristic composition variability at both the local and landscape scale (Feilhauer et al., 2013). On this basis, habitats may also be characterised regarding their 'weighted abiotic preferendum' using the species' indicator value first proposed by Ellenberg (Ellenberg et al., 1992; Chytrý et al., 2007).

In the present work, we suggest that the quality of grassland habitats can be efficiently evaluated by spectral information derived from remote sensing images. We chose to analyse the spectral information using supervised classification in order to enable the resulting classification to fit with the reference system used in the Habitat Directive (EC, 1992). Remote sensing then may allow an effective habitat monitoring in space (extension) and time (dynamics) at low cost. Such an approach may be particularly well suited for the French CarHAB (Cartographie des Habitats) program which aims to regularly monitor the vegetation throughout the French territory (Garroni Parisi, 2013).

Spatio-temporal dynamic monitoring of the floristic composition of plant communities is indeed urgently required to provide a dynamic evaluation of the vegetation community conservation status. Up to now, habitat maps produced within the Natura 2000 framework are generally based on photo-interpretation, a time consuming technique, requiring a large number of field data sets. As a consequence, this technique restricts the evaluation and monitoring of habitats to accessible and small areas (Zak, & Cabido, 2002). The use of satellite imagery appears promising to overcome these problems and together with field campaigns, these techniques increase the repeatability of the mapping: some attempts have already been made on broad vegetation types (Mayr et al., 2007; Harvey, & Hill, 2001) while Zak, & Cabido (2002) and Fanelli et al. (2005) were able to successfully map a large range of habitats. Despite these attempts, vegetation maps based on satellite imagery classification and that also fit the Natura 2000 typology remain scarce.

While we recognized that floristic continuum may occur and may be mapped (see Schmidtlein et al., 2007), habitats with particular protection status could be essential to distinguish for conservation purposes. In this perspective, considering vegetation units as clear habitats classes is thus

justified (Schmidtlein et al., 2007). This work then intends to map and thereafter monitor and report the conservation value of Natura 2000 vegetation units along space and time. Accordingly, vegetation units were defined as clear-cut units in reference to the Natura 2000 framework, i.e. the phytosociological classification of the vegetation.

This work pays special attention to the heterogeneity of the vegetation and how it may relate to the conservation status of the habitats. As biotic homogenisation is one of the main threats to biodiversity and conservation (McKinney, & Lockwood, 1999; Kühn, & Klotz, 2006; La Sorte et al., 2007), we investigated whether or not this phenomenon could be detected from a spectral data analysis. Spatial variation in environmental conditions within a landscape, and thereafter vegetation heterogeneity, is commonly recorded: for example, when subtle elevation contrasts control the flooding pattern (Amiaud et al., 1996) or when herbivore species control the grazing intensity (Loucougaray et al., 2004; Marion et al., 2010). Some studies (Palmer, 1994; Grace, 1999; Wilson, 2000; Lundholm, 2009) have suggested that plant species diversity is positively related to vegetation heterogeneity in the landscape. At a local scale, Marion et al. (2010) showed that vegetation heterogeneity explains up to 42% of the species richness in wet grasslands. The quantification of the level of vegetation heterogeneity is thus an important facet of vegetation to characterise within the Habitat evaluation process.

Palmer et al. (2002) suggested that spectral variation is related to the spatial variations of the environmental conditions and may be a proxy for species richness. A significant relationship between spectral heterogeneity and α-diversity, i.e. the diversity of species within a single sampling unit, has actually been found while the correlations remained low to intermediate (Gould, 2000; Rocchini et al., 2004; Rocchini, 2007). We thus choose to investigate the relationship between vegetation heterogeneity and species diversity by considering respectively: (1) the number of vegetation types recorded on the basis of the analysis of the spectral data set, as proposed by Rocchini et al. (2012), and (2) the α-species diversity of each vegetation unit obtained from field surveys. We studied the level of vegetation heterogeneity as suggested by Rocchini et al. (2012) and its between-years variation. Focusing on the vegetation units dominated by *Elytrigia repens*, which are species-poor and typical of poorly used grasslands, we aim to detect their possible expansion and the subsequent loss of species diversity in the landscape considered. We expected that the expansion of vegetation units dominated by *E. repens* will be accompanied by significant decrease in the level of vegetation heterogeneity.

The three objectives of this work were: (1) to produce a map of the various habitats (associations and their variations) occurring in an 3,000 ha large alluvial valley, based on SPOT-5 images analysed by supervised classification, (2) to investigate the relationships between species diversity of the vegetation and both its level of heterogeneity and between-years variation in the vegetation heterogeneity , (3) to identify if some variations of associations may be indicator of successional changes and thereafter assess whether or not the ongoing management fits well with

the conservation objectives.

Material and methods

Study site

The study site, named the 'Audubon's marshlands', is located in the Loire estuary (France), 30 km west of Nantes (1 ° 46'36.2" W, 47 ° 14'07.8" N) and is approximately 3,000 ha large. The landscape is mainly composed of natural grasslands managed by mowing, possibly followed by a second crop grazing, and grazing only. The maximum altitude is 4.51 m with a mean of 2 m. The mean precipitation and temperature between 1961 and 1990 were respectively equal to 741.3 mm and 11.7 ° C. The soil is mainly clayey. The site is flooded during the winter for one to three months and sometimes in the spring. It is thus mainly composed of meso-hygrophilous and hygrophilous grasslands.
During the spring of 2012, some hygrophilous areas of the study site were flooded by the river Loire. This event delayed cutting and in some cases prevented second-crop grazing. Consequently we only used meso-hygrophilous associations of the most elevated plots to compare the habitat diversity between years as they underwent the same flooding pattern during the two years of the study.

Satellite imagery

The methodological process followed in this study is summarized in the figure 4.2.

Two SPOT 5 images (©CNES 2011 and 2012, Distribution Spot Image S.A.) were acquired on 24th May 2011 and 23rd May 2012 with cloud-free conditions. To give priority to the resolution of the images as recommended by (Fanelli et al., 2005), and to respect the rule stating that pixels should be 2 to 5 times smaller than the area of the objects of interest (O'Neill et al., 1996), we selected the 2.5 m resolution with 3 bands (green, red, near infra-red) images. Each image was generated by pan-sharpening the multispectral bands (10 m resolution) with the panchromatic band (2.5 m resolution). Interestingly, Castillejo-González et al. (2009) showed that pan-sharpened images used in remote sensing provide similar results to those obtained from multispectral images. The images were pre-processed by the Centre National d'études Spatiales (France). This pre-processing consisted in geometrical correction, radiometric correction of distortions due to differences in the sensitivity of the elementary detectors of the viewing instrument, geometric correction of systematic effects (panoramic effect, Earth curvature and rotation) and radiometric distortion geometry.

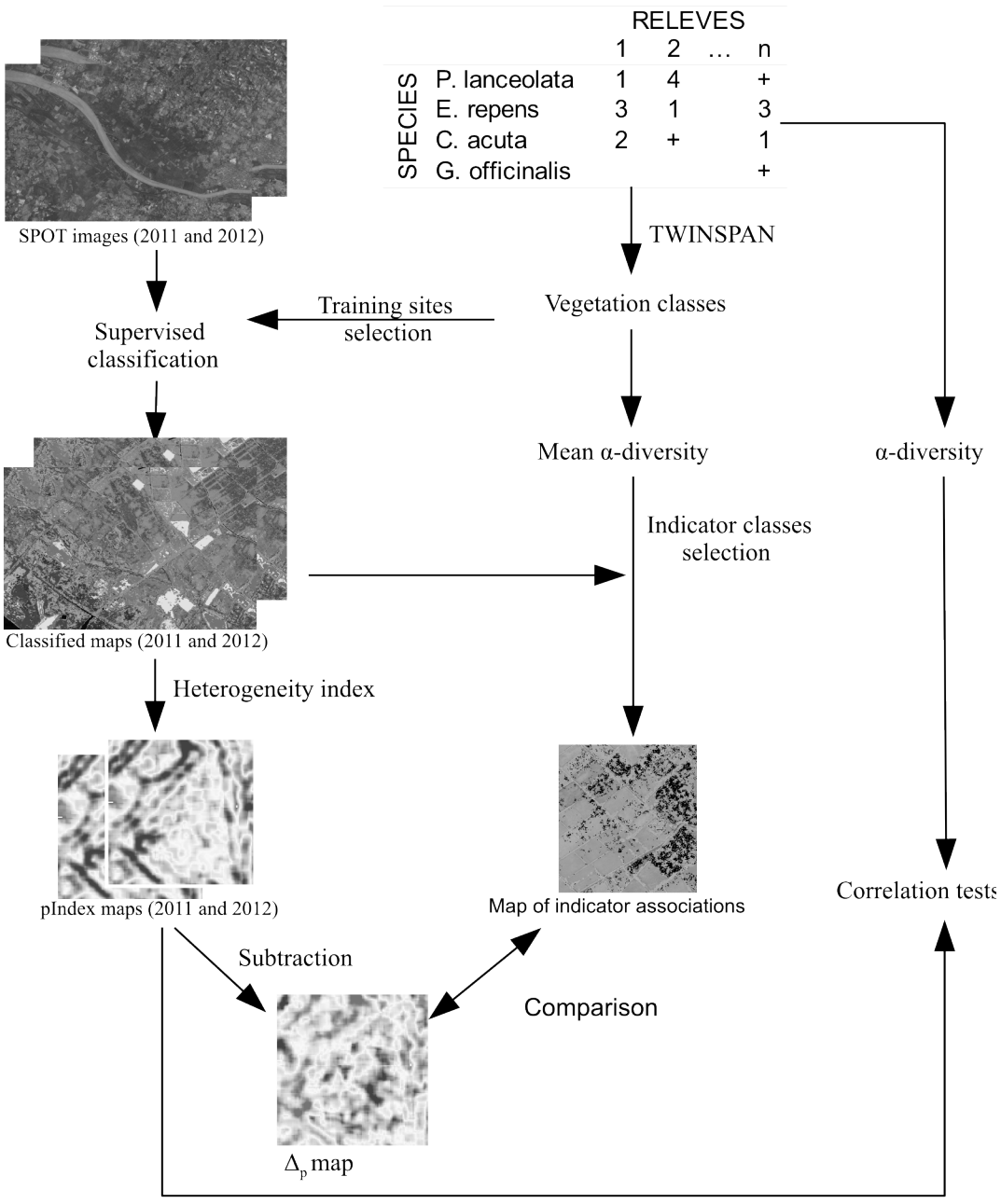

Figure 4.2 – Schematic flow chart illustrating the work flow of the analyses.

Phytosociological classification of vegetation and its between-year dynamic

Fifty-five phytosociological relevés were sampled in early June 2011, following the Braun-Blanquet method (Braun-Blanquet, 1928). Each relevé was carried out on homogeneous vegetation in a 16 m^2 plot (4x4 m) as recommended by Chytrý, & Otypkova (2003). The centre of each plot was geo-localised using differential GPS measurements (mean accuracy: 2.6 m) and the vegetation data were stored in Turboveg (Hennekens, & Schaminée, 2001). The relevés were classified by a Two-Way Indicator Species Analysis, TWINSPAN (Hill, 1979) using the JUICE software (Tichý, 2002).
The validity of the phytosociological discrimination of the relevés was tested by PERMANOVA on Braun-Blanquet coefficients with 999 permutations. Classes, i.e. a phytosociological associations or variations of association, were assigned to each relevé by considering their affinity with the typology proposed by Foucault (1984) up to the association and its variations (level).
The floristic composition of the same sites was monitored again in 2012 via a field campaign. To identify the vegetation units with particularly low α-species diversity, the Shannon α-species diversity level for every association and variation was compared using an ANOVA followed by Tukey's post-hoc tests with the Bonferroni correction for multiple comparisons of the means.

Vegetation mapping

One typical relevé per class was selected to be used as a training site for image classification. As the objective was to typified communities according to phytosociological reference, the typical relevé was chosen as the relevé with the closest floristic composition to the holotype of the corresponding association or variation of association. The holotype is the nomenclatural type defined by the International code of phytosociological nomenclature (Weber et al., 2000). To fit with this typology, the within class variability needs to be strictly limited. This will also be required in the aim of detecting subtle community variations within a given 'association' as they may indicate management changes. Each training site included the pixel containing the typical relevé and the four adjacent pixels.
Spectral separability of the training sites was tested using the Jeffries-Matusita distance (JMD) algorithm. The JMD was calculated for all paired training sites. The JMD ranges between 0 and 2. A JMD value > 1.9 is considered as an indicator for the spectral separability of the vegetation types (e.g. Thomas, & Noordhuis, 2002).

Following Zak, & Cabido (2002) and Fanelli et al. (2005), supervised classification was performed using training sites for which the floristic composition was known (see above). One supplementary class was used to take 'water' into account (a training site taken in the river "Loire" was used to run the supervised classification). The classification used minimum distance classifier (nearest neighbour approach) with the Malanahobis distance as dissimilarity metric distance, to

extrapolate the knowledge acquired during field work. The Mahalanobis distance was selected, since a preliminary test (not included in this paper) showed that the other classification algorithms produced lower heterogeneity levels, and consequently were less relevant with regards to the objectives of our study. The nearest class is assigned to each pixel of the image, producing a map of the spatial extent of each association over the study area (Zak, & Cabido, 2002). A classification threshold defining the Mahalanobis distance beyond which pixels were not classified was chosen. The distance was chosen quite low in accordance with the objective to restrict within-class variability and then stick to the typology approach chosen. To define this threshold, we first performed an unsupervised classification using k-means algorithm with 13 classes. Then we randomly sampled 1000 pixels in the study zone and calculated the mean Mahalanobis distance for each pairs of pixels related to a given class. For all the 13 classes, the mean Mahalanobis distance obtained from the analysis was close to two, and we accordingly selected this value as a threshold for classes separation. As a matter of fact, Hatten, & Parsley (2009) used the same Mahalanobis distance value.
Supervised classification was performed on the two SPOT images with training sites localised at the same place. For the 2012 image classification, we updated phytosociological classification of the training sites with vegetation relevés acquired during the 2012 field campaign.

Classification accuracy was assessed by crossing the results obtained for the 2011 image with a Natura 2000 Habitats map of the site (unpublished). This map was made in 2004 from a ground-observed habitat interpretation at the plot scale. A confusion matrix was derived from 160 validation plots, randomly selected (20 points per community). As the reference map was less accurate regarding the spatial scale and vegetation typology than our classification, some of the classes of plant communities that we distinguished were merged. We assumed that vegetation changes between 2004 and 2012 for the classes included in the confusion matrix were rather insignificant: indeed, we only considered associations and their variations related to micro-topography which remains unchanged along years. The performance of the method was assessed using the Kappa coefficient and global accuracy as suggested by Congalton (2001).
The accuracy of the 2012 classification was assessed using ground-truth plots acquired in 2012 (Figure 4.4). As we wanted to identify variation of associations which could be considered as indicator of successional changes, we only assessed change detection between 2011 and 2012 for *E. repens*-dominated classes.

Vegetation heterogeneity and its dynamic

Patches of vegetation were delineated on each SPOT-5 classification map using the 8-cells rule that considers all eight adjacent cells, including the four orthogonal and four diagonal neighbours. The number of patches belonging to each association was calculated for the 2011 and 2012 clas-

sifications. The patch frequencies among the associations were compared between 2011 and 2012 using chi-square tests.

The heterogeneity of the vegetation was measured at the landscape scale with the calculation of an heterogeneity index similar to the one proposed by Rocchini et al. (2012), in order to express the diversity of vegetation patches within a given area. This heterogeneity index was thereafter called the 'p Index', for 'patch heterogeneity index', and it was calculated using the information from the vegetation map developed in 2011 and in 2012. The p Index was calculated for each pixel using a 9-pixels side moving window as:

$pIndex = -\sum p_i * ln(p_i)$

where pi was the relative abundance of each phytosociological association (class) present in the window of the landscape considered (9 x 9 pixels, each 2.5 meters large) (Figure 4.3). The average p indices for the meso-hygrophilous areas were compared in 2011 and 2012 using a two sample Z-test for mean comparison.

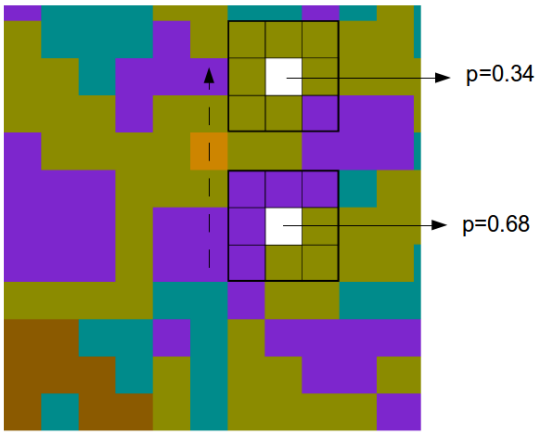

Figure 4.3 – The GRASS add-on r.diversity gives a p Index value for each central pixel of the moving window. It is applied to a thematic map of the vegetation obtained after supervised classification.

The correlation between α-diversity (i.e. the Shannon Index calculated from the vegetation relevés) and the value of the p Index of the pixel corresponding to the location of the relevés was studied using the Pearson's rank test with fifty three relevés carried out in 2011 and 2012. As a scale effect may intervene in the relation between landscape diversity and species diversity (Oldeland et al., 2010), correlations were tested for 10 different calculation windows from 3x3 pixels to 25x25 pixels.

Locating and monitoring low α-diversity patches

Focusing on a location where grazing/mowing did not occur in 2012 due to the long flooding, we tested the ability to detect the expansion of low α-diversity vegetation units and its consequence on the p Index value variation from 2011 to 2012. All new *E. repens* variations of associations which appeared in 2012 (i.e. not predicted in 2011 but predicted in 2012) were accordingly mapped. The between-years variation of the p Index value was calculated as $\Delta_p = p_{2012} - p_{2011}$.
The 2012 classification map was validated using the field surveys showing changes from 2011 to 2012 with new *E. repens*-dominated units.

Images were classified using ENVI 4.7. A landscape analysis (p Index and number of patches) was carried out using the GRASS GIS software (GRASS Development Team, 2012) with an r.diversity add-on (Rocchini et al., 2012). The number of patches was calculated using Fragstat 4. Statistical analyses were performed using the R software (R Development Core team, 2013).

Results

Phytosociological classification of vegetation and their diversity

A TWINSPAN analysis of the 130 relevés discriminated 13 relevé groups corresponding to the typical associations and their variations (Table 4.1), according to the typology proposed by Foucault (1984). Groups of relevés presented significantly different species compositions (PERMANOVA, $F = 6.69$, $P < 0.001$).

Table 4.1 – Synoptic table of the phytosociological relevés. For each association or variation of association, the species class frequencies (with a 20% interval) and median of cover (Braun-Blanquet scale) are provided in exponent format. Species with low frequencies (< 10%) and not typical of associations were removed. For each association, the mean Shannon Index ± standard deviation is given. GLYMAX: *Glycerietum maximae*, CARRIP: *Caricetum ripariae*, CARACU: *Caricetum acutae*, GLYFLU: *Glyceriteum fluitansis*, ELEOEN: *Eleocharo palustris-Oenanthetum fistulosae*, RANOE: *Ranunculo ophioglossifoli-Oenanthetum fistulosae*, RANOEly: *Elytrigia repens* variation of the *Ranunculo ophioglossifoli-Oenanthetum fistulosae*, HORLO: *Hordeo secalini- Lolietum perennis* (inf: inferior, sup: superior), SENOE m: *Senecio aquatici-Oenanthetum mediae* mown, SENOE $m + g$: *Senecio aquatici-Oenanthetum mediae* mixed, SENOEly: *E. repens* variation of the *Senecio aquatici-Oenanthetum mediae*, TRIOEN: *Trifolio squamosi-Oenanthetum silaifoliae*.

	GLYMAX	CARRIP	CARACU	GYFLU	ELEOEN	RANOE	RANOEly	HORLO inf	HORLO sup	SENOE c	SENOE m	SENOEly	TRIOEN
Glyceria maxima	V 4	II 3	I 2	III +									
Carex riparia	I +	V 3			I +								
Carex acuta	I 2		V 4		I 2								
Glyceria fluitans	III +	II 1		V 4	II +								
Eleocharis palustris	III 3	V 2	III 2		V 3	III +	I 3	II +					
Oenanthe fistulosa	I +	III +	III 1		V 2	II 2	II +	I 3					
Trifolium fragiferum		II +	IV 2		V 3	V 2	I +	II +	I 2				
Trifolium michelianum	I +		IV 2	I 4	III 1	III 2	V +						
Phalaris arundinacea	I 2	I 2	IV 1		III 2	III +	I +	III 2					
Alopecurus geniculatus	I 1	III 1	II +	III 1	IV 2	I 3	I 1	I +					
Ranunculus flammula	II +	III +	III 1		IV +	I 1							
Elytrigia repens			III 1		I 1	III 3	V 5		III 1	III 2	III 2	V 4	III 4
Agrostis stolonifera	IV 2	III 3	II 3	II 3	IV 2	IV 2	III 2	V 2	IV 2	III 2	IV 2	II +	II 2
Poa trivialis	I 2	III 2	IV 1	IV +	V 2	III 1	I +	V 2	V 2	III 3	IV 1	V +	III 1
Ranunculus repens		I 1	III +	II +	IV 1	III 2		IV 1		IV 1	III 2	III 2	
Senecio aquaticus			III +		III 1	V 1	IV +	II +	I +	V 3	IV 1	III 2	V +
Oenanthe silaifolia					IV +	V 1	II +	I +		IV 2	III 2	II +	V 1
Hordeum secalinum						II +	II +	V 3	V 3		IV 2	II +	IV 1
Lolium perenne					V +	V 2	I +	V 2	V 2	III 1	V 3	I 2	V 1
Alopecurus pratensis						III +	I +	III 1	III 2	V 1	IV +	IV 2	I +
Alopecurus bulbosus						II 1	IV 2	II 1	I 1		I 2		V 1
Trifolium maritimum						I 2	I 2		I 2		I +		V 2
Leontodon autumnalis									II 1	II +	III +	I +	I 2
Trifolium repens						II +	II +	V 1	III 2	I 1	II 1		
Cynosurus cristatus								I 1	II 2	I 2	II +		V 1
Gaudinia fragilis									II 1		I 1		V 1
Bromus racemosus								I +	I 1	II 2	I +	I 1	I 1
Cirsium arvense									II +	II 2	III 2	I +	I 1
Holcus lanatus							I 1	II +	I 1			V 1	
α-diversity ± s.e.	1.39 ±0.34	1.53 ±0.18	2.03 ±0.32	1.03 ±0.15	2, 30 ±020	2, 41 ±0.18	1, 35 ±0.23	2, 05 ±0.29	2, 22 ±0.21	2, 10 ±0.07	2, 39 ±0.13	1, 58 ±0.21	2, 12 ±0.52

Regarding the relationships with the flooding pattern, the *Glyceriteum maximae* association (GLYMAX), *Glycerietum fluitansis* association (GLYFLY), *Caricetum acutae* association (CARACU), *Caricetum ripariae* association (CARRIP), *Eleocharito palustris-Oenanthetum fistulosae* association (ELEOE) and *Ranunculo ophioglossifolii-Oenanthetum fistulosae* association were distinguished as hygrophilous associations linked to long winter flooding. *Hordeo secalini-Lolietum perennis*, *Senecio aquatici-Oenanthetum mediae* and *Trifolio squamosi-Oenanthetum silaifoliae* are recorded and constitute the meso-hygrophilous associations developing with short winter flooding conditions.

Recurrent variations within associations were found: one variation corresponded to patches dominated by *E. repens* and was encountered for both the *Senecio-Oenanthetum* (SENOEly) and the *Ranunculo-Oenanthetum* (RANOEly) associations. Two variations of the *Hordeo-Lolietum* association were identified according to the elevation (inferior: HORLO inferior/superior: HORLO sup) which contrast in terms of the soil wetness. Two variations of the *Senecio-Oenanthetum* association were found according to the management type: one variation corresponds to mowing (SENOE m), the other corresponds to a mixed management with mowing and grazing (SENOE m+g). The SENOEly association showed a significantly lower Shannon α-diversity than the other associations, i.e. mown and mixed variations of *Senecio-Oenanthetum* and *Hordeo-Lolietum* ($F = 37.95$; $P < 0.001$) (Table 4.1).

Vegetation mapping

The spectral signatures of the 13 vegetation classes distinguished were studied on thirteen training sites (one per group), with perfect spectral separability between each class (the JMD among all paired training sites was found to be equal to 2). The accuracy of the classification was good (overall Kappa index: 0.83, global accuracy: 85.6%), and was roughly similar for all associations. The map obtained after the supervised classification with a Minimum Distance classifier (Figure 4.4) was compared with the field-based vegetation map made in 2004. The map produced showed a high level of accuracy when compared with the field data (Table 4.2) with low commission (1 minus the probability that a sample classified on the map/image actually represents that category on the ground) and low omission errors (1 minus the probability of a reference sample being correctly classified).

Table 4.2 – Confusion matrix with a 2004 map produced by interpreting the ground-observed habitats. ELEOEN: *Eleocharo palustris-Oenanthetum fistulosae*; HORLO: *Hordeo secalini- Lolietum perennis* (inf: inferior sup: superior); SENOE c: *Senecio aquatici-Oenanthetum mediae* mown; TRIOEN: *Trifolio squamosi-Oenanthetum silaifoliae*, GLYMAX: *Glycerietum maximae*, GLYFLU: *Glycerietum fluitansis*, CARRIP/CARACU: *Caricetum rippariae* and *Caricetum acutae*.

		Classification results								Row total	Producer's accuracy	Ommission error
		ELEOEN	SENOE m	HORLOL inf	HORLOL sup	TRIOEN	GLYMAX	GLYFLU	CARRIP/CARACU			
Reference	ELEOEN	18		4				4	3	29	62.1%	37.9%
	SENOE m		17							17	100.0%	0.0%
	HORLOL sup	2		16	1	1				20	80.0%	20.0%
	HORLOL inf		1		18	3				22	81.8%	18.2%
	TRIOEN		2		1	16				19	84.2%	15.8%
	GLYMAX						19			19	100.0%	0.0%
	GLYFLU						1	16		17	94.1%	5.9%
	CARRIP / CARACU								17	17	100.0%	0.0%
	Col total	20	20	20	20	20	20	20	20	160		
	User's accuracy	90.0%	85.0%	80.0%	90.0%	80.0%	95.0%	80.0%	85.0%			
	Commission error	10.0%	15.0%	20.0%	10.0%	20.0%	5.0%	20.0%	15.0%			

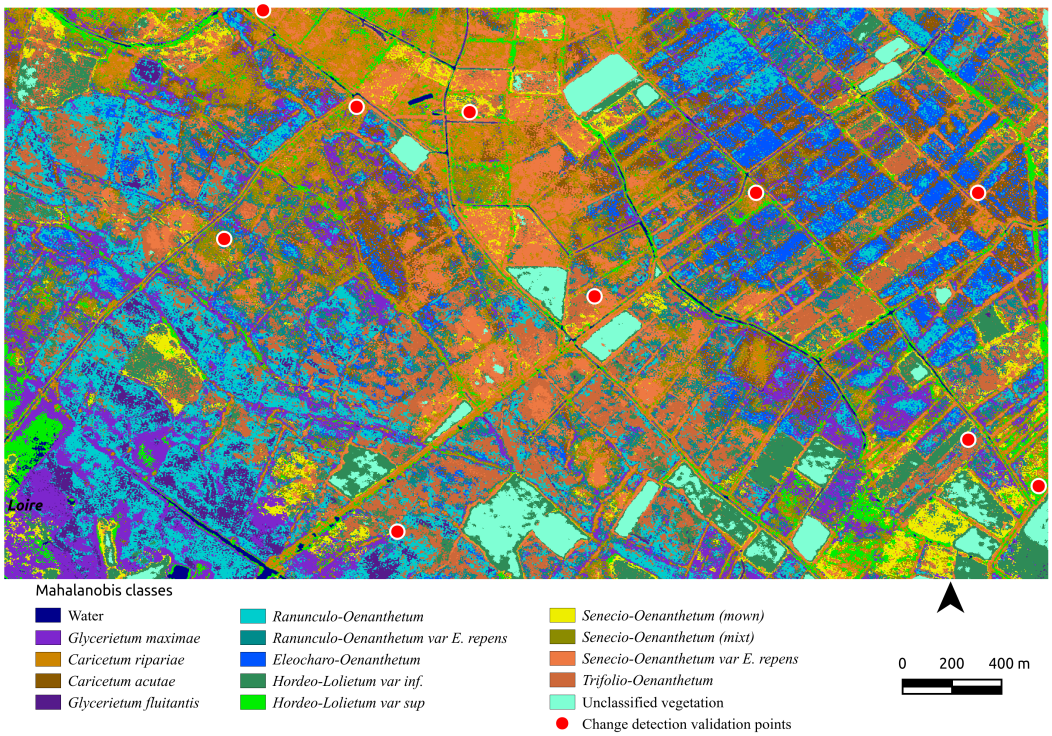

Figure 4.4 – Audubon's marshland cartography obtained by supervised classification (Mahalanobis).

Heterogeneity of the vegetation

In the meso-hygrophilous areas, the number of patches increased by 51.2% between the two years; this increase concerned all of the meso-hygrophilous associations distinguished ($\chi^2 = 3763.15$, $df = 3$, $P < 0.001$). The changes of larger magnitude occurred for the SENOEly and HORLO sup associations, for which the number of patches increased by +70.9% and +86.7% respectively from 2011 to 2012. Figure 4.5 shows the patches of the *E. repens* variations of *Senecio-Oenanthetum* which were predicted in 2012 in a field, where second-crop grazing did not take place in 2011. The patch number only decreased between 2011 and 2012 in the SENOE m association (-13.4%). The change in the SENOE vegetation from 2011 to 2012 was towards SENOEly for 41.7% of the patches when mown and for 49.9% of the patches when both grazed and mown.

Figure 4.5 – Localisation of the *E. repens* variation of *Senecio-Oenanthetum* (in orange) as it appeared in 2012 (zoom in a non-flooded zone).

Contrary to what was expected, no significant correlation was found between the p Index value, i.e. the diversity of the vegetation patches in the landscape, and the α-diversity of the vegetation, regardless of the scale investigated (Table 4.3).

The vegetation heterogeneity in the meso-hygrophilous areas, assessed by the mean p Index, increased from 0.72 to 0.80 between 2011 and 2012 (significant variation, $Z = 107.96$; $P < 0.001$). The Figure 4.6 shows the variation in the heterogeneity index between 2011 and 2012 and the resulting Δp ($p_{2012} - p_{2011}$) map where grazing/mowing did not occur in 2012 due to long flooding. In this context, the pixels were occupied by new *E. repens* pixels (cf. supra) and 30% were found to be accompanied by a decrease in the vegetation heterogeneity ($\Delta p < 0$) while 70% correspond to an increase in the vegetation heterogeneity ($\Delta p > 0$) (Figure 4.6 and 4.7).

Table 4.3 – Pearson correlation coefficient between heterogeneity index (pIndex) and Shannon index of diversity calculated for phytosociological relevés. Scale corresponds to calculation window size in pixel. (n.s. = non significant).

Scale	Correlation coeff
3x3	0.01 n.s.
5x5	0.16 n.s.
7x7	0.16 n.s.
9x9	0.17 n.s.
15x15	-0.01 n.s.
17x17	-0.04 n.s.
19x19	-0.03 n.s.
21x21	-0.01 n.s.
23x23	-0.01 n.s.
25x25	0.01 n.s.

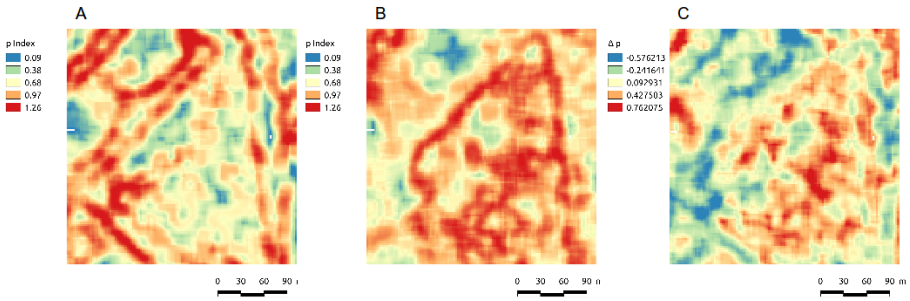

Figure 4.6 – Variation in the heterogeneity index between 2011 (A) and 2012 (B) of a parcel with low-intensity management in 2011. The p Index was calculated using a 9-pixel moving window. $\Delta p = p_2012 - p_2011$ (C).

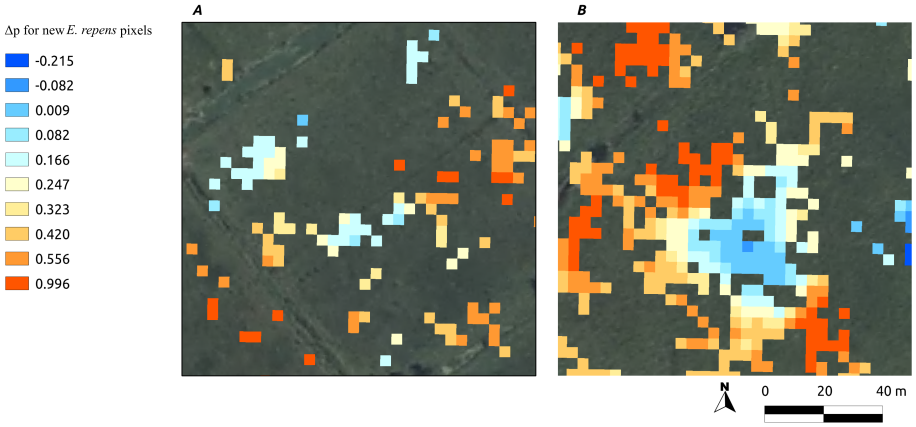

Figure 4.7 – Zoom in two parcels presenting colonisation by the *E. repens* variation of *Senecio-Oenanthetum* between 2011 and 2012. Δp values for the new pixels of *E. repens* variation of *Senecio-Oenanthetum* are displayed. A: Dispersed colonisation strategy (guerrilla); B: aggregated colonisation strategy (phalanx).

Discussion

Various remotely sensed data and classification types have been used to produce vegetation maps. For instance, Schmidtlein et al. (2007) used hyperspectral imagery to produce very fine-scale vegetation maps while Robin et al. (2010) mapped Madagascan mangroves using object-based classification on SPOT imagery. In our work, these two approaches were not selected. Indeed, hyper-spectral acquisition is too expensive to map large areas, as needed for the French national CarHAB program for example, and object-based classifications are less relevant than per-pixel classifications for our objectives. Besides, we wanted to test whether the 'salt and pepper effect' (Blaschke et al., 2000) could be used as a proxy for vegetation heterogeneity. We consequently performed per-pixel supervised classification on SPOT images.

Identifying vegetation units

Our study confirmed that phytosociological associations and their variations are distinguishable from spectral data, as first suggested by Zak, & Cabido (2002) and Fanelli et al. (2005). We obtained a perfect spectral separability between the vegetation classes defined, thanks to the very restricted intra-class variability: the classes are therefore as close as possible to their holotype relevé. The accuracy of the supervised classification was good probably due to the synchrony between both SPOT images and the phytosociological relevés that were made at the vegetation optimum as advised by Feilhauer, & Schmidtlein (2011). The results obtained in this study also confirm that monotemporal models are highly efficient in floodplain grasslands as suggested by Feilhauer et al. (2013). High resolution images (2.5 m) were chosen because resolution is considered to be even more important than spectral sensor characteristics (e.g Belluco et al., 2006))

and this resolution appears to be well adapted to detect grassy vegetation contrasts in structure and then to detect plant patches. A coarser spatial resolution would have produced mixed pixels resulting in an underestimation of the mapping accuracy (Xie et al., 2008) and together, would underestimate the spatial complexity, which is a key point in the habitat diversity assessment technique chosen. The minimum distance classifier based on the Malanahobis distance we used to performed the supervised classification has been found to produce maps with more than 80% overall accuracy (Govender et al., 2008; Perumal, & Bhaskaran, 2010).

Clues for the conservation status of the habitats

Mapping the variations of associations may effectively be used to assess the habitat conservation status (Feilhauer et al., 2013). Change detection by post-classification analysis is considered as a very effective technique (Mas, 1999). The change detection accuracy was found equivalent to the classification accuracy, as expected from Stow et al. (1980). Our approach may also detect potential α-diversity loss or gain as well as the spatial or temporal dynamics underneath that may notably relate to management. In our study, we showed that the *E. repens* variation of *Senecio-Oenanthetum* can be used as an α-diversity degradation indicator at the landscape level, as already reported by Loucougaray et al. (2004). The α-diversity loss observed may be related to the dominance of the community by the very competitive species *E. repens* (Ryel et al., 1996), which finally led to the exclusion of less competitive species (Amiaud et al., 1996; Bouzillé et al., 2010).

The ability to detect the increased extent of the poorly diverse *E. repens* variations at the expense of other more diversified associations constitutes a robust indicator of a decrease in α-diversity at the landscape level. This information is now available from remote sensing data as shown in our work and this constitutes a main strength of the approach suggested.

Heterogeneity from spectral data and the prediction of α vegetation diversity

Some authors have recently tested the hypothesis stating that spectral heterogeneity can be used as a surrogate of plant α-diversity (Palmer et al., 2002). Nevertheless, an important part of spectral heterogeneity is not related to changes in species compositions (Rocchini et al., 2007) but may rather reflect environmental (e.g. soil characteristics) and vegetation (e.g. phenology) variations, which do not systematically impact plant α-diversity. Rather than using spectral heterogeneity to approach α-diversity, the calculation of the heterogeneity index based on classes of habitats as we suggested (cf. the p Index) effectively accounts for vegetation contrasts which may be interpreted regarding habitat types, habitat variations and their associated α-diversity. However, we did not found any significant correlation between the p Index and the observed plant α-diversity at any scale. Such a poor correlation may be explained by the degradation of continuous quantitative information into discrete classes (Palmer et al., 2002). We also showed that the between-years variation with regards to the vegetation heterogeneity in the landscape may apprise managers of

possible α-diversity variations.

Diversity changes and management regime of the grasslands

In the studied grasslands, the number of patches predicted to be dominated by *E. repens* increased by more than 70% in two years. These changes may be related to management changes: the very late mowing that occurred the second year surely favoured *E. repens*. This species is favoured by the absence or low intensity of mowing and grazing (Amiaud et al., 2008). In such conditions, E. repens shows a high growth rate and clonal spreading with long-lived rhizomes (Benot et al., 2013).

Late mowing is practised in the Loire valley when the summer is very wet, like in 2011: in such conditions, farmers are prevented from mowing earlier and may not let the cattle graze in late summer and autumn. The observed decline in the plant diversity in grasslands with low use of the biomass (only one crop grazing or mowing) had been recorded in other grasslands (Amiaud et al., 1996) and is corroborated by local farmers.

Species diversity at the landscape scale and the heterogeneity of the vegetation

New *E. repens* pixels, predicted in 2012 in a calculation window impact the Δp value as it constitutes a new vegetation unit in the studied window of the landscape. The expectation is that the heterogeneity level, approached via Δp, will be increased. Actually, the results showed that the direction of the change is quite variable from one situation to another (Figure 4.6) and mainly depends on the spatial pattern of the *E. repens* expansion. New *E. repens* pixels accompanied by a positive Δp were usually isolated and might correspond to *E. repens* colonisation with a 'guerrilla strategy' colonization (i.e. individuals presenting ramets with long spacers) (Lovett-Doust, 1981; Ryel et al., 1996; Amiaud et al., 2008). They might also correspond to cowpats or grazing-refusal (during second-crop grazing). They represent the dominant strategy (70% of the new *E. repens* pixels).

New *E. repens* pixels related to a negative Δp, i.e. corresponding to a decrease in the heterogeneity of the vegetation in the 'window' considered, are mainly aggregated in large patches. They might correspond to aggregated colonisation, the so-called 'phalanx strategy' (Amiaud et al., 2008), with individuals presenting ramets with short spacers.

The coexistence of these two colonisation strategies is in accordance with the findings presented by Amiaud et al. (2008), who showed that *E. repens* shifted from a 'guerrilla strategy' to a 'phalanx strategy' depending on the grazing intensity. However, regardless of the situation, *E. repens* patches correspond to a decrease in the α-diversity in the 'window' and this may lead to either an increase or a decrease in the p Index value.

However, clear variation in the heterogeneity of the vegetation (i.e. in the p Index value) remains an easy, although rough, proxy to detect changes from the remote sensing facilities and

thereafter locate the place where the field visits are the most informative regarding the conservation status.

The approach we detailed here will make it possible to map vegetation and habitats distinguished up to the plant association variation level. Combined with good field data (i.e. plant relevés), the powerful remote sensing tools will then provide accurate information regarding the vegetation units that are presented, the vegetation heterogeneity and the species diversity at various spatial scales.

Importance relative de la gestion et des facteurs environnementaux comme déterminants de la richesse spécifique et de l'abondance d'arthropodes et de végétation

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Cette section est présentée sous la forme d'un article soumis dans la revue *Naturwissenschaften*: Lafage D. & Pétillon, J. Natural, stochastic disturbance vs. human-induced management of biodiversity: the effectiveness of agri-environmental schemes in flooded meadows. *Naturwissenschaften*, révision modérée.

5.1 Résumé

Pour faire face à la perte de biodiversité liée à l'intensification des pratiques agricoles, l'Union Européenne à mis en place des mesures incitatives visant à encourager les exploitants à mettre en œuvre des pratiques respectueuses de l'environnement : les mesure Agro-Envionnementales (MAE).

Malgré l'importance des sommes engagées, peu d'études ont essayé d'évaluer l'impact des mesures prises sur des groupes non-cibles. En outre, comme nous l'avons vu dans le chapitre 2, les perturbations, et plus particulièrement les inondations, sont reconnues comme étant de puissants facteurs influençant les communautés animales et végétales. Cependant, aucune des études menées afin d'évaluer l'efficacité des MAE ne l'a été dans un contexte d'écosystème soumis à de tels facteurs de forçage.

L'objectif de cette étude est donc d'évaluer l'impact des MAE (globalement et pour chaque type de mesure) sur les diversités et densités d'arthropodes et de plantes dans les prairies inondables de la Vallée de la Loire et des Basses Vallées Angevines.

Quatre-vingt trois prairies soumises ou non à inondations hivernales et de printemps ont été inventoriées par "suction sampling" (araignées et carabiques) et relevés phyosociologiques (végétation).

Trente-sept paires de prairies ont été utilisées pour évaluer l'impact global de la contractualisation (R-ANOVA) et 83 pour tester l'impact du retard de fauche et de la limitation de la fertilisation (GLM) en incluant les effets indirects et directs des inondations.
Aucun effet de la contractualisation n'a été mis en évidence sur les diversités et les abondances d'araignées, de carabiques et de végétation. A l'inverse, des effets à long terme de l'humidité ont systématiquement été décelés, soulignant le rôle clé de l'inondation dans ces écosystèmes. Notre étude plaide donc pour une reconsidération attentive de l'efficacité des MAE dans des habitats stochastiquement perturbés.

5.2 Relative importance of management improvement and natural disturbance in flooded agro-ecosystem

Abstract

In Europe, Agri-environment schemes (AES) have been implemented to counteract the effects of agricultural intensification. Studies investigating the role of management improvement induced by (AES) are quite numerous but rarely take into account the effect of natural perturbations such as flooding although severe disturbances are well known to shape community structure. Here we investigated the relative importance of management improvement and flooding in explaining the diversity of two dominant arthropod groups and vegetation in alluvial meadows.
Sampling took place in 2013, using suction samplers for arthropods and phytolosociological relevés for vegetation, in 83 meadows distributed along 200 km of the Loire Valley (France). Pair-matched approach (by R-ANOVA) was used to assess overall effects of AES, whereas a gradient analysis (GLM) was carried out to assess the impact of AES prescriptions (fertilisation and cutting-date) together with indirect and direct effects of flooding.
No significant effect of AES was found on arthropod density and diversity, or plant productivity and diversity. The only prescription impact was the positive effect of high-amounts of fertilisers on spider diversity. Conversely, systematic long-term effects of flooding were found on all response variables of spiders, carabids and plants, underlining the key role of this factor in alluvial meadows. Our study demonstrates that maintaining or enhancing hydrological functioning of ecosystems can be even more important than improving management for conservation purposes in flooded habitats.

Introduction

Over the last decades, agricultural intensification has accelerated adverse effects on wildlife. In Europe, Agri-environment schemes (AES) have been implemented to counteract these effects by providing financial incitement for farmers to adopt extensive agricultural practices. Farmers involved in AES preferentially engage fields which are less suitable for intensive farming (Kleijn, & Zuijlen, 2004) explaining why semi-natural grasslands are especially engaged by farmers.
Investments in AES are substantial, with 34.9 billion Euros planned for 2007-2013 programmes (COM, 2008). They currently cover 21% of all farmlands in the 27 EU countries. Despite these high financial inputs, AES seem to have contrasting successes (Kleijn et al., 2006), depending on the AES type and the model studied. For example, AES are recognised to have positive effects on birds in the UK (Brereton et al., 2007) and on pollinators in Switzerland (Albrecht et al., 2007) but AES also prove damaging when poorly designed or targeting single interest (Konvicka et al., 2007). Conversely, results on plant diversity are usually reported to be positive (Critchley et al., 2004; Kleijn et al., 2001). Monitoring and evaluation of these schemes are finally imperative to improve their efficiency and maximize the conservation outcomes.
Evaluation of AES impact usually focusses on birds (Kleijn et al., 2006; Kleijn et al., 2001; Marshall et al., 2006) and vegetation (Critchley et al., 2004; Knop et al., 2005) mainly because they are the main targets of AES as arthropods are often neglected in biodiversity conservation policies (e.g. Cardoso et al., 2011). Some studies also dealt with arthropods, mainly bees and grasshoppers (Kleijn et al., 2001; Marshall et al., 2006; Knop et al., 2005), and found positive effects of AES. Despite their recognised indicator value in agricultural landscapes, predator arthropods like spiders and carabid beetles remain poorly studied in the context of AES.
Flooding is a key driver of intertidal and riverine ecosystems, and particularly of arthropod communities (Desender, & Maelfait, 1999) and vegetation (Violle et al., 2007). Nevertheless, no study has assessed the efficiency of AES in such systems shaped by stochastic disturbances. Here we evaluated the efficiency of AES on two non-target groups (spiders and carabids) and vegetation in the flooded meadows of the river Loire (France).

Material and methods

Study area and sampling design

The study site covered 200 km of the Loire Valley (France: Figure 5.1). Land is mainly covered by hay meadows with an extensive hedgerow network. Meadows are usually cut in early- or mid-summer with second-crop grazing. The study site included four AES zones with various prescriptions regarding cutting-date and fertilizers. Cutting-dates were between 5th June to 20th July, within four defined classes: free (not under AES), before 20th June, between 20th June and

1st July, after 1st July. Fertiliser prescriptions were 0, 30 or 60 unit/Ha. Almost all meadows are flooded during winter, but in 2012 and 2013, the study sites were also flooded during spring.
Carabids and spiders were sampled in eighty-three hay meadows during June 2013. Suction sampling (a standard technique providing quantitative data on arthropods: Brook et al., 2008) was realised using a 12.5 cm diameter intake placed on the ground. At each sampling site, 5 samples (20 x 15s suctions) were taken (total area: 0.12 m^2/sample). Samples were stored in 70% alcohol and taken to the laboratory for sorting and identification to species level. One phytosociological relevé per sampling site was made in a 16 m^2 plot. Vegetation biomass was approximated Enhanced Vegetation Index (EVI: Lafage et al., 2014b) measured during 16 days by LP DAAC (product MOD13Q1).

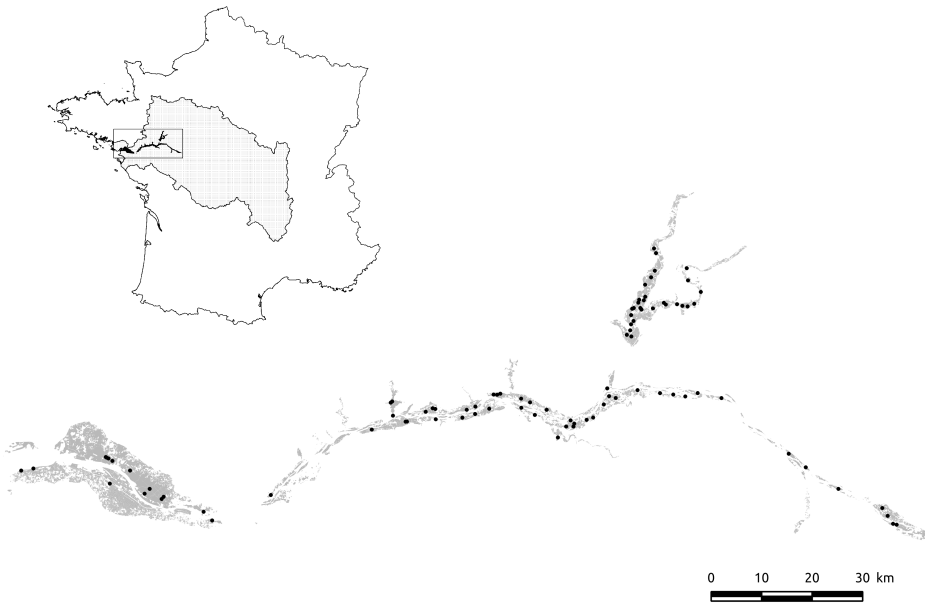

Figure 5.1 – Localisation of the study sites in the Loire watershed (France). Gray surfaces indicate meadows and black dots correspond to the sampled meadows.

Statistical analysis

Spatial autocorrelation, tested using Moran's I, was low enough (Table 5.1) to be neglected (Gerisch et al., 2012). Spatial patterns in response variables were also searched, but they were not significant (Table 5.2).

Table 5.1 – Autocorrelation tests (Moran's I) for mean estimated richness and density of carabids and spiders and plant productivity and diversity.

	Spiders	Carabids	Plants
Estimated species richness	$I = 0.109$; $P < 0.001$	$I = 0.011$; $P = 0.660$	
Density	$I = 0.245$; $P < 0.001$	$I = 0.001$; $P = 0.612$	
Shannon Index			$I = 0.08$; $P = 0.011$
EVI			$I = 0.07$; $P = 0.027$

Table 5.2 – Significativity of MEM tests for arthropod and plant diversities and densities.

	Spiders	Carabids	Plants
Estimated species richness	$P = 0.15$	$P = 0.680$	
Density	$P = 0.230$	$P = 0.300$	
Shannon Index			$P = 0.240$
EVI			$P = 0.300$

Arthropod species richness was estimated for each sampling site using the average of four non-parametric estimators based on species incidence: Chao1, Jacknife1, Jacknife2 and Bootstrap. Vegetation diversity was estimated by the classical Shannon index. A paired sample approach (with or without AES) was used to test the overall AES effect on density and diversity of spiders and carabids, and on plant productivity and diversity. Repeated analyses of variance (R-ANOVA) were performed between sites located less than 1km from each other and presenting similar abiotic conditions (see similar designs in previous studies on AES effiency: Kleijn et al. (2006), Knop et al. (2005), and Scheper et al. (2013)).

Responses of arthropod diversities and densities and vegetation productivity and diversity to cutting-date (four classes) and fertiliser inputs (three levels) were tested using Generalised Linear Models (GLMs) with quasi-Poisson distribution and a stepwise model selection by AIC. A variable describing whether or not the site had been flooded during spring 2013 (i.e. binary variable for short-term effects of flooding) and a moisture gradient (i.e. discrete variable for long-term effects of flooding) were also included in the GLMs. Five moisture classes were defined from low (1) to very high (5) according to the mean Ellenberg indicator value of each vegetation type (defined by a Two-Way Indicator Species Analysis). As flooding was expected to influence the effects of cutting-date, and fertiliser amounts to be influenced by flooding, interactions between those variables were also included. Statistical analyses were performed using the R software (R Development Core team, 2013) with vegan (Oksanen et al., 2013), MASS (Venables, & Ripley, 2002) and PCNM (Legendre et al., 2013) packages.

Results

No significant effect of AES, site, or interaction between AES and site was found on estimated spider and carabid species richness and densities, or on plant productivity and diversity (Table 5.3).

Table 5.3 – Means ± s.e. of response variables for fields under or not AES with F and P value for fixed factor (contract), site factor and their interaction (R-ANOVA).

		AES	Free	Contract		Site		Interaction	
		Mean± s.e.	Mean ± s.e.	*F*	*P*	*F*	*P*	*F*	*P*
Spiders	Density	2.24 ± 1.84	1.83 ± 1.19	0.96	0.338	2.12	0.158	0.04	0.838
	Esimated species richness	14.74 ± 7.14	10.50 ± 3.97	3.98	0.06	0.24	0.630	0.143	0.709
Carabids	Density	1.02 ± 1.01	1.64 ± 1.47	1.53	0.228	0.06	0.804	0.05	0.833
	Esimated species richness	2.08 ± 2.40	3.45 ± 3.46	1.13	0.298	2.47	0.129	0.10	0.760
Plants	Shannon Index	2.15 ± 0.42	2.24 ± 0.37	0.19	0.667	2.08	0.162	0.02	0.883
	EVI	5366.47 ± 1187.46	5135.07 ± 1096.789	0.31	0.594	0.29	0.594	1.43	0.243

No direct (short-term) effect of flooding and no interactions between flooding and prescriptions were found, indicating that the impact of prescriptions, if any, was not influenced by flooding (Table 5.4).

Table 5.4 – Means ± s.e. of response variables for fields under or not AES with F and P value for fixed factor (contract), site factor and their interaction (R-ANOVA).

Group	Response	Variables kept	*F*	*P*
Spiders	Estimated species richness	Fertilisers	4.28	0.008
		Moisture	4.45	0.003
		Fertilisers : Vegetation type	1.92	0.101
	Abundance	Fertilisers	3.33	0.024
		Moisture	1.75	0.150
		Fertilizers : Vegetation type	1.99	0.090
Carabids	Estimated species richness	-	-	-
	Abundance	Fertilisers	1.16	0.330
		Moisture	2.89	0.028
		Fertilisers : Vegetation type	2.11	0.074
Plants	Shannon Index	Cutting date	0.03	0.993
		Fertilisers	1.21	0.303
		Moisture	7.47	< 0.001
	EVI	Cutting date	0.03	0.993
		Fertilisers	1.21	0.303
		Moisture	7.48	< 0.001

The only significant impact of prescriptions on the six response variables was the effect of fertiliser amount on estimated spider species richness (Table 5.4). Sites under AES with 60 kg/ha nitrogen had higher estimated spider species richness (Figure 5.2a). Fertilisation also had a significant effect on spider density (Table 5.4), but post-hoc tests revealed no significant difference among input levels.

Long-term (indirect) effects of flooding systematically influenced density and diversity of arthropods, and productivity and diversity of vegetation. Sites with low moisture (classes 1 and 3, i.e. with less frequent floods) presented higher estimated spider species richness than sites with very high moisture (class 4) (Fig. 5.2b). Sites with very high moisture (class 5) presented higher carabid densities than sites with low moisture (class 2) (Figure 5.2c). Plant productivity was positively influenced by flooding (Table 5.4), with higher EVI in moister sites, although differences between means were not significant. Plant diversity of sites with high moisture (Class 4) was significantly lower than sites with very high moisture (Class 5), medium moisture (Class 3) and low moisture (Class 1: Figure: 5.2d).

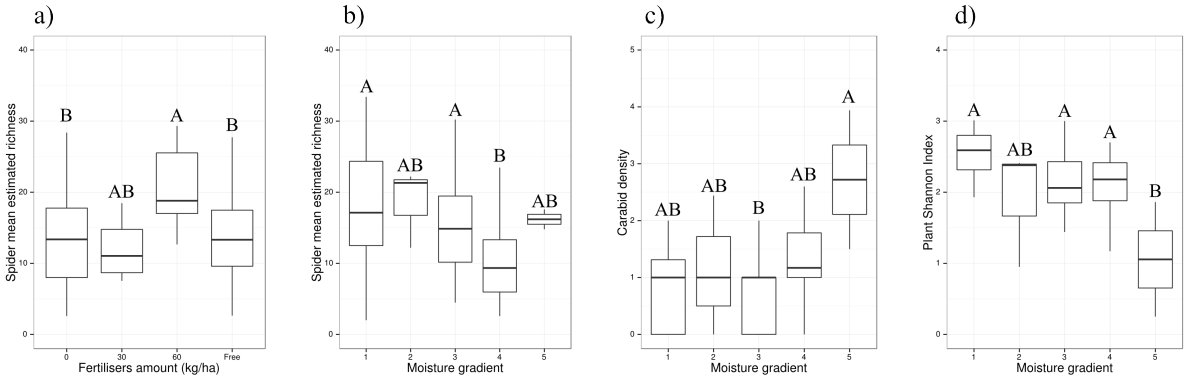

Figure 5.2 – GLM selected by the stepwise selection for spider and carabid density and estimated richness and plant productivity and diversity.

Discussion

Overall, our results demonstrated no significant impact of AES when compared to large-scale disturbances like flooding. Flooding systematically drove both species richness and densities/biomass of all studied taxa, which can be easily explained by its large spatial extent (including both AES and non-AES meadows) and its duration (here several months). The absence of difference between meadows with or without AES is yet in accordance with some previous studies in non-flooded habitats, dealing with spiders (Marshall et al., 2006; Knop et al., 2005), carabids (Marshall et al., 2006) and plants (Kleijn et al., 2001; Marshall et al., 2006), but the existence of different levels in AES prescriptions could lower the impact of the most binding AES.

Conversely to the biodiversity-productivity theory (Grime, 1973), sites fertilised with 60 kg/ha nitrogen supported highest spider diversity. Besides, sites not under AES were no different from sites with medium or low nitrogen inputs. This is in accordance with studies (Lafage et al., 2014b; Patrick et al., 2008) suggesting a 'bottom-up' control of arthropod diversity. The lack of fertilisation effects on spider and carabid densities could be explained by a threshold effect. Indeed, fertiliser inputs remained low, even in fields not under AES contract, as winter floods input large quantities of organic matter. Fertilisation restrictions had no effect on plant species diversity, whereas significant reduction is usually observed even for low levels (Plantureux et al., 2005). Nevertheless, in flooded grasslands, no effect of fertilisation on plant diversity was reported under 90 kg/ha/yr (Bonis et al., 2008).

Delaying cutting-date had no impact on the three groups, in accordance with recent studies on spiders and carabids (Lafage, & Pétillon, 2014a) but in opposition with studies on plants. Indeed, maximum plant diversity is usually observed for late cutting-dates (mid-June to mid-July) in European grasslands (Critchley et al., 2007). Flooding might be a stronger driver of vegetation and arthropod communities. We found that flooding had long-term effects (demonstrated by the moisture gradient) on spider and plant diversities and on carabid density. Flooding had contrasting effects, depending on the response variables, with basically positive effects on carabid density and plant productivity and deleterious effects on species richness (which is in accordance with previous works, e.g. on intertidal spiders and plants: Desender, & Maelfait, 1999; Pétillon et al., 2010).

Our results suggest that management improvement has few, almost no, effects on arthropods and plants compared to those induced by a prolonged flooding. Conservation actions in such ecosystems might have to focus on maintaining or enhancing hydrological functioning. Because natural meadows are in constant regression by conversion to intensive agriculture (Millennium Ecosystem Assessment 2005), AES can yet be considered an efficient way of maintaining a rarefied habitat, despite their limited efficiency in flooded systems.

Importance relative des facteurs locaux et paysagers comme déterminants des diversités α et β d'arthropodes et de végétation

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Cette section est présentée sous la forme d'un article à soumettre à la revue *Œcologia*.
Lafage D., Bouzillé J-B., Maugenest S. & Pétillon J. Disentangling the influence of local and landscape factors on α and β diversities: opposing responses of plants and ground-dwelling arthropods in wet meadows.

6.1 Résumé

Nous avons démontré au cours de ce travail que les assemblages d'espèces d'araignées, de carabiques et de plantes étaient structurés par des facteurs agissant aussi bien à l'échelle locale qu'à large échelle. C'est à cette dernière qu'interviennent les facteurs paysagers. Ces facteurs comprennent la nature du paysage mais aussi sa connectivité. Plantes, araignées et carabiques sont connus pour être influencés par les facteurs paysagers. Cependant l'importance relative de ces derniers dans la structuration des assemblages d'espèces, et plus particulièrement sur les composantes de diversité, est encore peu connue.
Dans ce chapitre, nous avons donc étudié grâce aux partitions de variance, l'influence relative des facteurs locaux et paysagers (composition et connectivité) sur les diversités α et β (elle-même partitionnée en "replacement d'espèces" et "variation du nombre d'espèce") des trois groupes. Nous avons aussi cherché à vérifier l'hypothèse selon laquelle la diversité β d'un groupe est fonction de sa capacité de dispersion.
Nous avons ainsi montré que la diversité α de plantes dépend principalement de facteurs locaux alors que celle d'araignées et de carabiques dépend de facteurs paysagers (respectivement composition et connectivité).
La part de diversité β des trois groupes liée à des variations de nombres d'espèces s'est révélée négligeable. La diversité β de plantes dépend majoritairement de facteurs locaux alors que celle

d'araignées dépend de facteurs paysagers (à parts égales : composition et connectivité). De façon surprenante la diversité β de carabiques dépend à parts égales de facteurs locaux et paysagers (connectivité).
Nous n'avons pas mis en évidence de différences de diversité β entre les trois groupes, ce qui, associé à l'importance du remplacement d'espèce, suggère une capacité de dispersion des groupes équivalente dans le paysage concerné et / ou une faible connectivité.
Ainsi, pour gérer efficacement les prairies inondables, il convient d'intervenir non seulement à l'échelle locale mais aussi à large échelle en intervenant sur le paysage, sa composition et sa connectivité.

6.2 Disentangling the influence of local and landscape factors on α and β diversities: opposing responses of plants and ground-dwelling arthropods in wet meadows

Abstract

Agro-ecosystem biodiversity is threatened by the intensification of agricultural practices and landscape homogenisation. Understanding the key drivers of species diversity in these ecosystems is essential to counteract such threats. Identifying whether the factors determining diversity at varying scales differ among biological taxa is thus a key, although less investigated, topic.
In this study, we assessed the relative importance of local and landscape (i.e. composition and connectivity) variables in explaining α- and β-diversities (species turnover and nestedness) of three highly diverse groups, differing in mobility and dispersal: plants, spiders, and carabids. Sampling took place in 2013, using suction samplers for arthropods and phytosociological relevés for vegetation, in 77 hay meadows distributed along 200 km of the Loire Valley (France). We found plant α-diversity to be driven by local factors, whereas spider and carabid α-diversities were mostly determined by landscape factors (by composition and connectivity, respectively). Nestedness was negligible for the three groups. Plant β-diversity was also mainly influenced by local factors, whereas spider β-diversity was driven by landscape factors (composition and connectivity, equally). Surprisingly, carabid β-diversity was mainly influenced by local factors and landscape connectivity. Despite these differences, plant, spider, and carabid β-diversities were not different, suggesting comparable dispersal abilities and/or a low connectivity at large scale, which is in accordance with the high species turnover observed here. Managing biodiversity in meadows consequently necessitates acting at local and landscape scales, the first targeting plants and the second arthropods.

Introduction

A large number of studies have tried to understand de determinants of local species-richness, i.e. α-diversity (Jiménez-Valverde et al., 2010). Studies dealing with β-diversity are considerably less numerous (McKnight et al., 2007) but their number has increased in the recent years (e.g. Boieiro et al., 2013; Braaker et al., 2013; Hendrickx et al., 2007). α-Diversity describes within-habitat diversity (MacArthur, & Wilson, 1967) and is mainly driven by local processes (Whittaker, 1972). β-Diversity, or between-habitat diversity (Magurran, 2004), is believed to respond to two models: (1) the niche model which states that species sorting is linked to species requirements; (2) the model which states that species sorting is linked to dispersal across the landscape (Nekola, & White, 1999). Thus β-diversity is generally thought to be driven by local and landscape factors, yet the impact of local and landscape factors on α- and β-diversities seems to vary between groups (e.g. Báldi et al., 2013; Duflot et al., 2014) and habitats studied (Jeanneret et al., 2003).For instance, plant species richness response to landscape diversity has been found to be negative by Roschewitz (2005), positive by Weibull et al. (2003) and null by Dauber et al. (2003) and Krauss et al. (2004).

In agro-ecosystems, meadows are considered to be the most species-rich habitat (Noordijk et al., 2010; Woodcock et al., 2011) and have been proven to be an important source of diversity for crops (Benton et al., 2003; Purtauf et al., 2005). Plants and arthropods are a key component of meadow ecosystems, particularly spiders and carabids that can play a role in pest control (Symondson et al., 2002). However, the intensification of agricultural practices has led to a serious impoverishment of species diversity with the introduction of damaging practices (Marshall et al., 2006) and landscape homogenisation (e.g. Strijker, 2005; Tscharntke et al., 2005). In Europe, agri-environment schemes (AES) have been implemented to counteract these effects by providing financial incentives for farmers to adopt environmental-friendly agricultural practices. AES seem to have varying success (Kleijn et al., 2006; Lafage, & Pétillon, 2014b) depending on the AES type and the model studied. Indeed some studies recently suggested that landscape factors could have a higher impact on species diversity than management practices (Batáry et al., 2008; Weibull et al., 2003), lowering the effect of agricultural practices improvement. Understanding the relative importance of local and landscape factors on α- and β-diversities is thus essential to design effective measures to promote biodiversity in agro-ecosystems. Further, assessing the relative contributions of local versus regional processes is considered essential in understanding global patterns of species diversity (Huston, 1999).

Here, using variance partitioning, we disentangled the influence of local and landscape (composition and connectivity) variables on α- and β-diversities of three biological model groups varying in (short-distance) mobility and (long-distance) dispersal: two groups of macro-arthropods (spiders and carabids) and plants in meadows of the Loire Valley.

Due to the lack of mobility of plants, we first expected α-diversity of plants to be more driven

by local factors than that of spiders and carabids. In wet meadows, seed dispersal is reported to be low outside of flood events, and we consequently expected β-diversity of plants to be more determined by local than landscape factors (well-known role of local filters), and also to be higher than that of the two other groups (due to increased turnover). Lastly, due to their long-distance dispersal abilities, we expected diversities of spiders and carabids to be mostly driven by landscape factors, but mainly shaped by landscape connectivity for carabids (active dispersal) and by landscape composition for spiders (passive dispersal). The relationship between structuring factors and biological groups was also investigated with an explanatory approach using multivariate analyses of species composition of the three studied taxa.

Due to differing dispersion abilities and mobility, we expected the relative importance of local and landscape factors to differ among groups, especially regarding β-diversity. For plants, little is known about the influence of the surrounding landscape and its relative importance (Marini et al., 2008). For animals, the ability of individuals to disperse among local communities may be an important determinant of species turnover and nestedness, where species with low dispersal ability are strongly influenced by increasing habitat isolation (Hendrickx et al., 2009). Thus, we expected spider and carabid β-diversities to be mainly influenced by landscape connectivity, and plant β-diversity by local conditions. Indeed, Weibull et al. (2003) found species richness of butterflies, carabids, rove beetles, and spiders to generally increase with landscape heterogeneity on a farm scale. On the other hand, Öberg et al. (2007) found Linyphiidae (a spider species) diversity to be more sensitive to local habitat type. Finally, due to differences in dispersal capacities, we expected spider and carabid β-diversities to be lower than plant β-diversity.

Material and methods

Study area and sampling design

Study area and sampling design

The study site covered 200 km of the Loire Valley in Western France (Figure 6.1). Land is mainly covered by hay meadows and poplar groves. The hedgerow network is prominent. Hay meadows are cut in early or mid-summer and usually grazed by cattle in autumn.
Carabids and spiders were sampled in 77 hay meadows along the study area. Sampling was carried out from the on 1-28 June 2013, between 10.00 and 17.00, when weather was dry. Suction sampling was realised using a suction sampler with a 12.5 cm diameter intake placed onto the ground. At each sampling site, 5 samples were taken. Each sample consisted of 10 x 15 s suctions (total area: 0.12 m^2/sample). Samples were stored in 70% alcohol in the field and taken back to the laboratory for sorting and identification to species level. Suction sampling is a standard technique to provide quantitative data (Brook et al., 2008).

One phytosociological relevé per site was sampled, following the Braun-Blanquet method (Braun-Blanquet, 1928). Each relevé sampled homogeneous vegetation in a 16 m^2 plot (Chytrý, & Otypkova, 2003).

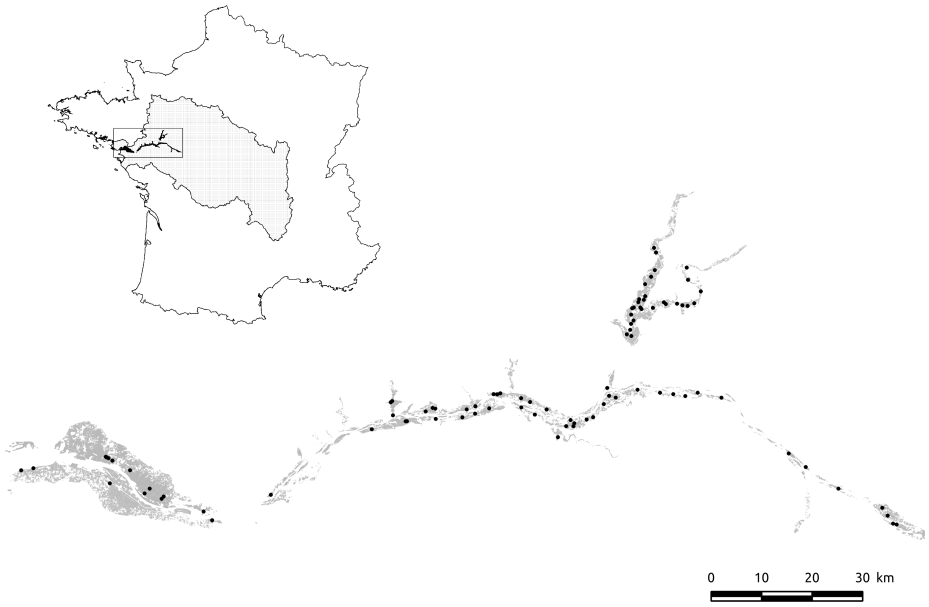

Figure 6.1 – Localisation of the study sites in the Loire watershed (France). Gray surfaces indicate meadows and black dots correspond to the sampled meadows.

Environmental characteristics

Three variable sets supposed to affect arthropod and plant diversities were defined. The first variable set comprised eight variables describing local conditions. Two variables relevant for spiders described habitat conditions determined by vegetation: mean litter depth (ten measurements to the next cm per sampling plot) and mean vegetation height (ten measurements to the next cm per sampling plot). Soil characteristics were defined using mean Ellenberg indicator values (Ellenberg et al., 1992) for moisture, nutrient level and exposure to light. One variable described whether the site had been flooded during spring 2013 (i.e. a binary variable for the short-term effects of flooding). Two variables described local meteorological conditions (mean temperature and precipitation during the sampling month).

The second set of variables corresponded to landscape composition regarding land-cover and geology. It included the four dominant land-cover types (grasslands, woods, water, urbanisation) defined at four different scales using buffers (100, 200, 300 and 400 m). It also included soil type (arena, granite, gneiss, mica, clay, shale, chalk). Land cover types and hedgerows (see after) were retrieved using photo-interpretation of satellite imagery (BD Ortho IGN 2008 and 2009) (Vaudelet, 2008). We retrieved soil type from the Simplified Lithographic Map provided by the Bureau de Recherches Géologiques et Minières (BRGM).

The third variable set, characterised connectivity. It included three variables describing meadows localisation: distance to the sea (longitudinal connectivity), minimum distance to the river Loire (lateral connectivity) and minimum distance to an hedgerow. It also included landscape heterogeneity, estimated using the Landscape Shannon Diversity Index (SHDI), using same four buffers used for the landscape data set. SHDI was calculated using the QGIS plugin LecoS (Jung, 2012). Landscape closure was estimated using beta index (BI) of connectivity (beta= number of hedges / number of nodes). Area of the field was also included in this dataset. Finally, variables describing spatial patterns in arthropod communities at different scales were researched. We used Moran's eigenvector maps (MEM) (Legendre et al., 2013), see Braaker et al. (2013) for a detailed description.

Statistical analyses

Spider and carabid species richness (α-diversity) were estimated for each sampling site using the average of four non-parametric estimators based on species incidence: Chao1, Jacknife1, Jacknife2 and Bootstrap. β-Diversity was estimated through a dissimilarity matrix (corresponding to Sørensen pair-wise dissimilarity) partitioned into its two components: species turnover (β_t) and nestedness (β_n) following Baselga (2010) and using the betapart R package (Baselga, & Orme, 2012).

To ensure that buffer scale fits to group requirements, we performed simple regressions on each variable and selected the radius with lowest AIC value for each landcover and connectivity variable,

and each response variable.

Variables shaping arthropod and plant α-diversities were defined using multiple regressions with a stepwise model selection procedure by AIC (Akaike, 1974), implemented in the MASS R package (Venables, & Ripley, 2002). Linear, logarithmic, inverse, quadratic, cubic, power, compound, logistic, growth, and exponential regression were compared and the model with the highest R^2 was selected. Relative contribution of explicative variables to the model was estimated using relaimpo package (Grömping, 2006) with the R^2 contribution averaged over orderings among regressors (Chevan, & Sutherland, 1991; Lindeman et al., 1980).

To test for differences in β-diversities among groups, multiple-site dissimilarity matrices were computed using the betapart package for R (Baselga, & Orme, 2012) and Simpson dissimilarity index. We then performed a re-sampling procedure in the β-diversity matrix (50 pairs of sites were randomly sampled 50 times) to perform multiple comparison tests.

To identify variables significantly explaining arthropods and plant β-diversities, similarity matrices corresponding to species turnover were regressed against environmental variables using the Canonical Analysis of Principal Coordinates (CAP) implemented in the vegan package (Oksanen et al., 2013) for R. The environmental model was built with a forward selection procedure, using CAP, on the environmental dataset to select significant variables ($P = 0.05$ after 9999 random permutations) to explain variation in dissimilarity matrices. Variance partitioning was then performed on the selected variables using the vegan package (Oksanen et al., 2013). Variables expressed in proportion (landcover) were arcsine-transformed and surface variables were log-transformed to fit with normal distribution. To investigate possible differences between groups, spider, carabid, and plant drivers of species assemblages were investigated using constrained analysis. Following Legendre, & Gallagher (2001), species activity-densities were transformed to a Bray-Curtis distance matrix prior to analyses. The choice between redundancy analysis (RDA) and constrained correspondence analysis (CCA) was made according to the axis length of a detrended correspondence analysis (DCA). In the analyses, the distance matrix was the response variable and the environmental variables were the predictors. Monte Carlo tests with 999 permutations were carried out to test the significance of the selected environmental factors and constrained analyses axes.

Results

A total of 6,036 spiders belonging to 97 species, 383 carabids belonging to 43 species and 181 plant species were sampled. Spider and carabid assemblages were dominated by small aerial dispersers: 78% of spiders were Linyphiidae and 78% of carabids were small winged species.

The MEM analysis did not reveal any significant spatial pattern in the spider ($P = 0.15$), carabid ($P = 0.68$) or plant ($P = 0.24$) diversities and thus were not included in the connectivity data set.

Variables affecting arthropod and plant α-diversities

Overall, our models significantly explained plant, spider and carabid α-diversities ($R^2 = 0.63$, $P < 0.001$; $R^2 = 0.52$, $P < 0.001$; $R^2 = 0.30$, $P < 0.001$, respectively).
Local variables explained most α-diversity variance in plants (54.90%, Figure 6.2). Mean nutrient index was the main local factor (39.42% of variance explained) and was negatively linked to α-diversity (Table 6.1). The fraction of spider and carabid α-diversities explained by local factors was moderate to null (22.86% and 0%, respectively). Spider α-diversity was mostly negatively affected by moisture (15.8% of variance explained).
Landscape composition variables were the best predictor of spider and carabid α-diversities (54.09% and 57.93% of relative variance explained, respectively; see figure 6.2). Soil type was the main factor explaining spider, carabid and plant α-diversities (32.5%, 44.01% and 18.28% of variance explained, respectively).
Finally, connectivity explained moderately α-diversity of spiders and plants (23.05%, and 21.70%, respectively), with BI as the most important factor positively affecting spider α-diversity and negatively affecting plant α-diversity. Connectivity explained 42.07% of relative variance in carabid α-diversity, with the BI as the most important factor with a positive effect.

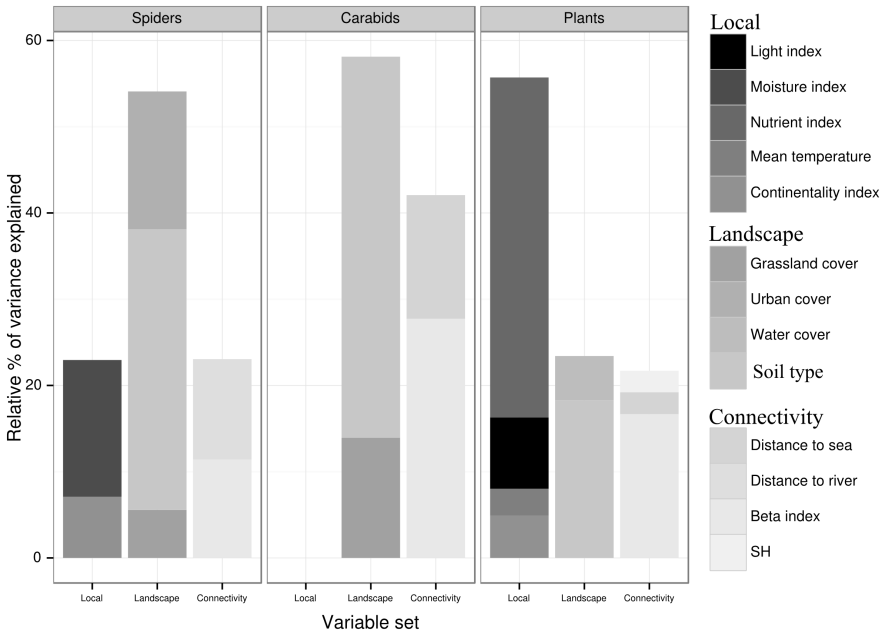

Figure 6.2 – Relative % of variance explained by each variable for spider, carabid and plant α-diversity.

Table 6.1 – Impact of local, landscape and connectivity variables on spider, carabid and plant α-diversities based on results of multiple regression followed by stepAIC. F, P and slope values are only displayed for variables kept by the stepAIC.

	Spiders			Carabids			Plants		
	F	P	Direction	F	P	Direction	F	P	Slope
Mean vegetaion height									
Litter depth									
Mean temperature				2.45	0.010	+			
Precipitations	2.56	0.010	-				3.67	0.01	-
Mean moisture index	2.64	0.010	-				4.21	0.01	-
Mean continentality index							3.35	0.01	+
Mean light index							4.21	0.01	+
Mean nutrient index							2.19	0.01	-
Flooding				4.78	0.010	-	3.39	0.01	-
Grassland cover									
Urban cover	2.99	0.010	+				1.83	0.03	+
Water cover									
Wood cover									
Soil type	1.37	0.050		1.73	0.010		1.59	0.01	
Area									
Distance to the sea				2.21	0.060		4.11	0.01	+
Distance to the river				2.09	0.020	-	5.27	0.01	-
Min distance to hedge							4.44	0.01	-
Bocage length							2.79	0.02	+
Beta index of connectivity							2.09	0.03	+
Index of heterogeneity	2.43	0.010	+				2.31	0.01	+

Group β-diversity comparison

Spider β-diversity was 0.97, corresponding to β_t=0.95 and β_n=0.02. Carabid β-diversity was 0.95, corresponding to β_t=0.92 and β_n=0.03. Plant β-diversity was 0.96, corresponding to β_t=0.95 and β_n=0.01. β_n of the three groups was thus considered negligible and was not included in further analysis.

We did not find any differences in β-diversities between the three groups ($\chi^2 = 46.34$, df = 47, $P = 0.499$).

Variables affecting arthropod and plant β-diversities

The first nine axes of the CAP on plant β-diversity were significant and explained 51.43% of species turnover. The first four axes of the CAP on spider β-diversity were significant and explained 20.55% of species turnover. The first three axes of the CAP on carabid β-diversity were significant and explained 31.46% of species turnover.

Variance partitioning revealed that local factors mainly affected plant β-diversity (43.75% of rel-

ative variance, Figure 6.3c). Plant β-diversity was negatively affected by precipitation, by all Ellenberg indicators tested and flooding (Table 6.2).

Spider β-diversity was mainly affected by landscape composition variables (30.77% of relative variance, Figure 6.3a), i.e. positively by urban cover and by soil type (Table 6.2). Including interactions with local and landscape composition variables, connectivity was the second driver of spiders β-diversity (30.76% of relative variance). Landscape heterogeneity also positively influenced spider β-diversity.

Carabid β-diversity was influenced by local factors (38.46% of variance explained) i.e. positively by mean temperature. Including interactions with local and landscape composition variables, connectivity was the second driver of carabids β-diversity (38.46% of relative variance). Distance to the river negatively influenced carabid β-diversity.

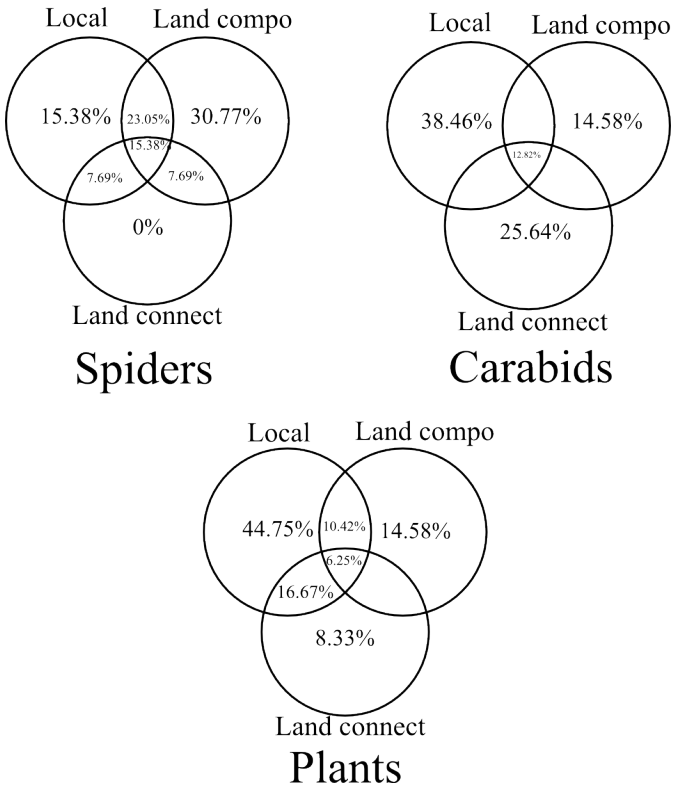

Figure 6.3 – Relative percentage of variance explained by each variable for spider, carabid and plant β-diversity (Venn diagram). Land compo: Landscape composition, Land connect: Landscape connectivity.

Table 6.2 – Impact of local, landscape and connectivity variables on spider, carabid and plant β-diversities based on results of multiple regression followed by stepAIC. F, P and slope values are only displayed for variables kept by the stepAIC.

		Spiders		Carabids		Plants	
		F	P	F	P	F	P
Local	Mean vegetation height						
	Litter depth						
	Mean temperature	1.63	0.010	2.71	0.010	1.98	0.020
	Precipitations	2.16	0.010			2.76	0.010
	Mean moisture index	1.91	0.025			7.34	0.010
	Mean continentality index					2.64	0.010
	Mean light index					3.14	0.010
	Mean nutrient index					2.81	0.010
	Flooding			5.53	0.010	1.93	0.010
Landscape	Grassland cover						
	Urban cover	2.53	0.010			1.84	0.020
	Water cover						
	Wood cover						
	lithography	1.56	0.010	2.24	0.010	1.47	0.010
	Area			3.56	0.010		
Connectivity	Distance to the sea			2.56	0.020		
	Distance to the river	1.75	0.025			2.16	0.010
	Min distance to hedge						
	Beta index of connectivity					1.80	0.020
	Index of heterogeneity						

Variables determining species assemblage composition

CCA on spider assemblages explained 42.9% of the total variance, with the first three axes of the CCA significant (all with $P = 0.005$). Variables explaining spider species composition were mainly moisture and distance to nearest hedge and soil type (Figure 6.4).

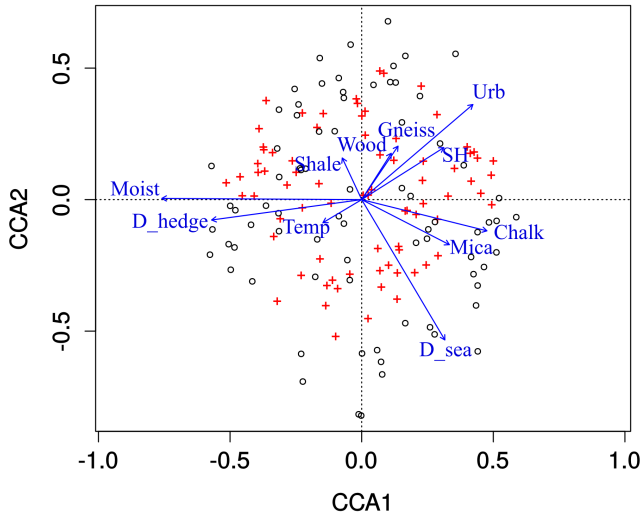

Figure 6.4 – Projection of significant variables from the CCA on spider species' Bray-Curtis distances. Sites are represented by crosses, and species by circles. Urb: % Urbanisation; Wood: % woodland; D_sea : $distancetosea$; $Temp$: $Meantemperature$; D_hedge : $distancetothenearesthedge$; $Moist$: $Ellenbergindexofmoisture$.

RDA on carabid assemblages explained 57.59% of total variance, with the first two axes of the RDA significant ($P = 0.05$ and $P = 0.02$, respectively). The main variables explaining carabid species composition were flooding, moisture, and distance to nearest hedge (Figure 6.5).

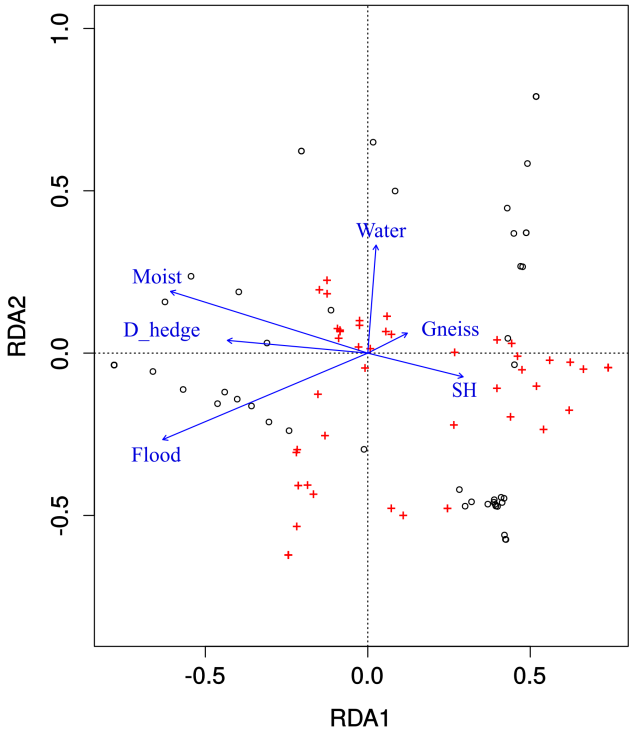

Figure 6.5 – Projection of significant variables from the RDA on carabid species' Bray-Curtis distances. Sites are represented by crosses, and species by circles. D_hedge : $distancetothenearesthedge$; $Moist$: $Ellenbergindexofmoisture$; SH : $heterogeneityindex$; $Water$: $\%water$; $Flood$: $sitefloodedornot$.

RDA on plant assemblages explained 54.8% of total variance, with the first six axes significant ($P = 0.005$, $P = 0.005$, $P = 0.005$, $P = 0.005$, $P = 0.01$, $P = 0.013$, respectively). Main variables explaining plant species composition were moisture, nutrient, distance to the river, and distance to the nearest hedge (Figure 6.6).

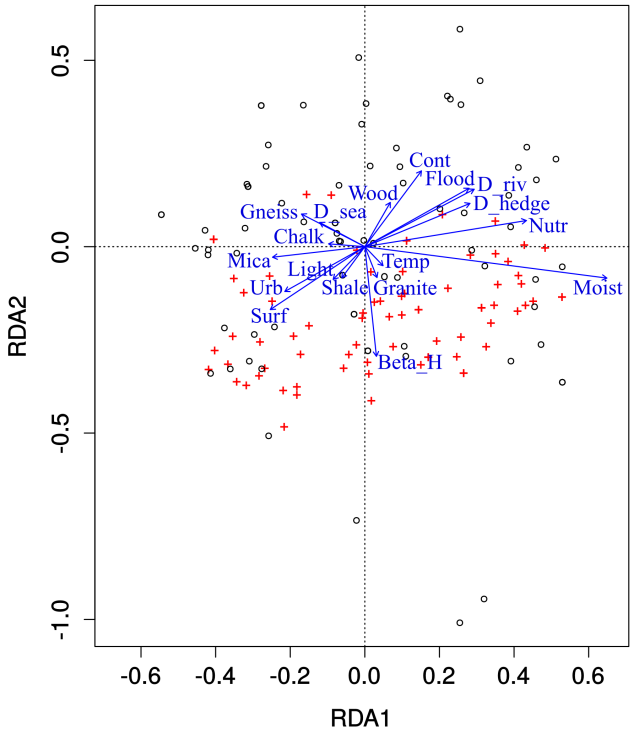

Figure 6.6 – Projection of significant variables from the RDA on plant species' Bray-Curtis distances. Sites are represented by crosses, and species by circles. Wood: % woodland; Cont: Ellenberg index of continentality; D_riv : $distancetotheLoireRiver$; D_hedge : $distancetothenearesthedge$; $Nutr$: $Ellenbergindexofnutrient$; $Moist$: $Ellenbergindexofmoisture$; $Temp$: $meantemperature$; $beta_H$: $heterogeneityindex$; $Surf$: $Surface$; Urb : $\%Urbanisation$; $Light$: $Ellenbergindexoflight$; D_sea : $distancetothesea$; $Flood$: $sitefloodedornot$.

Discussion

Our study demonstrated that local factors better explained plant α-diversity whereas spiders and carabids α-diversities were more determined by landscape factors (composition and connectivity). Nevertheless, variables affecting species assemblages were quite similar for the three groups and consistently included soil moisture and distance to the nearest hedge.

Plant α-diversity was primarily explained by soil nutrient index. This is in accordance with the numerous studies demonstrating that soil enrichment negatively influences plant α-diversity (e.g. Grace, 1999). Furthermore, local characteristics such as abiotic environment (Bennie et al., 2006; Sebastia, 2004), and other soil characteristics (Critchley et al., 2002), have been demonstrated to influence plant species richness.

Among local variables, spider α-diversity was most sensitive to the moisture index. This is also in accordance with numerous studies demonstrating that soil moisture is an important driver of

spiders assemblages (e.g. Entling et al., 2007).
Spider and carabid α-diversities were best explained by landscape composition. α-Diversity of the two groups was mainly affected by soil type. For carabids, this could be explained by the influence of soil structure — which is itself partly determined by soil type — on their larval phase (Blake et al., 2003). Our findings for spiders were in opposition to previous studies, which did not find any influence of soil type on spider communities (Coulson, & Butterfield, 1986; Sanderson et al., 1995). Spider diversity was also positively affected by urban cover, although to as lesser extent. In intensive agro-ecosystems, landscape composition is usually considered a limiting factor for spider species richness (Benton et al., 2003; Purtauf et al., 2005). Conversely, in a landscape extensively dominated by hay meadows, we found urban cover to be a potential source of new spider species. As a large part of spider assemblage was composed by Linyphiidae (78% of individuals), which passively disperse through ballooning, it follows that ubiquitous species usually found in urbanised zones, could have successfully colonised meadows. Landscape effect on spiders diversity is still under debate as it may depend on the habitat under study (Jeanneret et al., 2003). For instance, Batáry et al. (2008) found no impact of landscape on spider richness in Hungarian pasture, whereas other studies have positiveky demonstrated its effect on species richness in crop fields, fallow lands, and woodlots (Drapela et al., 2008);Öberg et al., 2007; Pluess et al., 2010; Schmidt, & Tscharntke, 2005; Schmidt et al., 2005.

Carabids are usually considered more sensitive to landscape than spiders. However, our results suggest that spider α-diversity is more influenced by landscape composition whereas carabid α-diversity is more influence by landscape connectivity. For the three groups, the BI was the main variable affecting species diversity among the connectivity variables tested. This index, reflecting the landscape's enclosure by a hedgerow network was expected to have a positive impact on arthropod and plant α-diversities by allowing the presence of woody species and facilitation of movements between suitable habitats (Burel, 1989; Miyashita et al., 2012; Purtauf et al., 2005; Weibull et al., 2003). In this instance, our hypotheses were confirmed for spiders and carabids but not for plants. This might be a result of a limited capacity of woody plants to colonise grasslands. For instance, Łukasz, & Sadowska, 1997 found an optimum diversity 3m away from the edge between forest and grassland.

We also observed that Linyphiidae and Harpalini dominated the assemblages of carabids and spiders. This dominance of small species could first be attributed to a sampling effect, although suction sampling is usually recommended to quickly obtain a representative sample of epigeic arthropod communities (e.g. Duffey, 1974). In fact Mommertz et al. (1996) considered it an inefficient way to sample large arthropods (such as Carabidae and Lycosidae). However, Brook et al. (2008) considered it an efficient technique to sample arthropods, including Carabidae with sufficient sampling effort. We consequently explain the dominance of small aerial dispersers as a

consequence of stochasticity of the environment due to flooding (Zulka, 1994).

In our study, the β-diversity link to nestedness was very weak for the three groups, and contrary to our expectations, we did not find any difference in species turnover rate between the three groups. Interestingly, the main driver of plant, spider, and carabid species assemblages was linked to hydrological conditions (moisture and flooding). This could induce similar β-diversities of the three groups, with such an important driver acting on assemblages in the same way. In addition, the importance of species turnover suggests either low landscape connectivity for the groups studied, or similar dispersion capacities of the three groups in this particular landscape. Considering the well-known (long-distance) dispersal abilities of plants, spiders and carabids, which have also been reported in alluvial meadows, we suggest that they were not limiting, and that the high turnover is more likely explained by weak landscape connectivity. Here, distance to the nearest hedge was indeed one of the main factors influencing species assemblages of the three groups. Whereas the hedgerow network could be considered a movement facilitator for some animals (Beier, & Noss, 1998), it can also act as a physical barrier for dispersion (Larrivée, & Buddle, 2009), especially of ballooning spiders (which represent 78% of individuals cached) and small carabids (85% of individuals cached) as demonstrated in the Loire valley by Lafage et al. (2014a). It also suggests that a species' pool is composed of generalist species and presents low functional diversity, which is the case in our study. Interestingly plant species assemblages were also driven by the distance from the meadow to the Loire river, suggesting use of hydrochory. In any case, as we only sampled hay meadows, we did not expect a high level of nestedness in β-diversity. Given the very low contribution of nestedness in total -diversity, we chose not to include it in further analysis. This decision was also motivated by the ongoing debate on β-diversity partitioning. Indeed, Almeida-Neto et al. (2011) suggested that only species turnover estimated by Baselga (2010) is usable.

Species turnover was mainly influenced by local factors for carabids and plants. As expected, local abiotic conditions (assessed by Ellenberg indicator values) explained plant β-diversity, with moisture as the dominant factor. Logically, mean precipitations and flooding were also variable negatively affecting plant β-diversity. Among local variables carabid β-diversity was only affected by mean temperature, which is in accordance with previous studies (Gillingham et al., 2012). Among landscape composition variables, soil type influenced all group β-diversities. Nevertheless, spiders were the most sensitive group to landscape composition including urbanisation which had a positive effect on species turnover. This is in agreement with the numerous studies which have found soil type to be an important driver of arthropod and plant species turnover (carabids: Blake et al. 2003; spiders: Churchill 1998; plants: Janssens et al. 1998; Gabriel et al. 2006).
Surprisingly, the area of the patches was not a key driver of arthropod and plant diversity. The landscape under study might not be sufficiently fragmented to produce an effect. Generally, in fragmented landscapes, patch area and shape complexity are important factors determining species

diversity within patches (Fahrig, 2003; Yamaura et al., 2008).
As expected connectivity was an important driver of carabid and spider β-diversity. Indeed, landscape openness is considered a dispersal trait filter for carabids, with highly mobile (small, macropterous) carabid species selected with increasing connectivity (Duflot et al., 2014). As previous studies found ballooning behaviour to be dependent of landscape heterogeneity (Bonte et al., 2006) we expected spider β-diversity to be positively influenced by landscape heterogeneity. Pure connectivity variables did not explain a significant portion of spider β-diversity. Nevertheless interactions between the BI and local and/or landscape variables explained an important part of spider β-diversity confirming the results of Bonte et al. (2006). Our findings are also in accordance with Jonsen, & Fahrig (1997) which found generalist insects diversity to increase with habitat diversity.

Overall, spider diversity appeared more sensitive to landscape composition, carabid diversity to landscape connectivity, and plant diversity to local factors. Thus, managing biodiversity in meadows implies acting at both the local and landscape scales, the former with and eye towards plants, and the latter toward arthropods. However managers have to be aware that improving connectivity through hedgerow networks could be a brake to biodiversity enhancement, as we found it could be for spiders and carabids.

Discussion générale et perspectives

Considérations méthodologiques

Techniques d'échantillonnage

L'activité-densité estimée par piège d'interception est très dépendante de la mobilité des individus (Cattin et al., 2003). Le piège barber a donc tendance à sous-échantillonner les espèces peu mobiles telles que les Linyphiidae (Mommertz et al., 1996). A l'opposé, l'aspirateur thermique semble, selon certains auteurs, sous-échantillonner les gros individus (Mommertz et al., 1996).
Dans notre étude, les résultats obtenus quant aux déterminants de la structuration des assemblages sont cohérents entre les deux méthodes et pour la plupart en accord avec la bibliographie existante. Les assemblages échantillonnés par les deux techniques sont cependant très différents. En effet, malgré un effort d'échantillonnage supérieur à celui recommandé par Brook et al. (2008), la proportion de lycoses et de carabiques de taille moyenne à grande est plus faible avec l'aspirateur thermique (seulement 2% de lycoses contre 80% au barber et 15% de carabiques de tailles moyenne à grande contre 95% au barber). Cependant, les échantillonnages utilisant cette technique ayant eu lieu sur des secteurs différents et après deux années consécutives de crues de printemps, des effets site, crue, météorologie ou stochasticité sont eux aussi très probables. Il est ainsi très difficile d'avancer une explication aux différences constatées.
A notre connaissance, seules les études de Mommertz et al. (1996) et Standen (2000) ont comparé l'efficacité du piégeage d'interception et du piégeage par aspiration. Cependant, les deux études ne portent que sur un nombre restreint de sites (respectivement 4 et 2) et Standen (2000) a comparé le piégeage par barber au piégeage par D-VAC + filet fauchoir. Nous proposons de comparer pièges barber et aspirateur thermique sur un nombre plus important de sites (10 parcelles tirées aléatoirement sur le secteur d'étude) permettant de disposer d'une large gamme de densité de végétation, facteur essentiel influençant l'efficacité des deux techniques (Thomas et al., 2006; Brook et al., 2008). Sur chaque parcelle, 3 pièges seront posés durant 2 X 15 jours. Lorsque les pièges seront relevés, 55 aspirations de 15 secondes sur une surface de 5 m^2 seront réalisées à proximité de chaque piège (mais à 5 m au moins du piège). Les assemblages d'espèces seront alors comparés en termes de diversité (spécifique et fonctionnelle) par GLM et de composition par PERMANOVA. Les tests devraient aussi être pratiqués en pâtures.

Plans d'échantillonnage

L'ensemble des études menées à l'échelle locale, l'ont été sur le site de l'Île Saint-Aubin. Bien que de véritables répliquats aient été utilisés pour chaque parcelle (Chapitre 1 et 3), le fait que parcelles et traitements soient confondus et que les expérimentations n'aient été réalisées que sur un site, pourrait être considéré comme une forme de pseudo-réplication au sens d'Hurlbert (1984). Cependant, comme l'avance Oksanen (2001), l'échantillonnage de véritables répliquats peut se révéler particulièrement coûteux et difficile à mettre en œuvre d'un point de vue technique. Dans le cas qui nous concerne dans le chapitre 3, trouver plusieurs parcelles proches, voire contiguës, ayant des niveaux topographiques (et donc une humidité et une végétation) comparables mais présentant des dates de fauche différentes s'est révélé être un véritable challenge. Nous devions de plus obtenir l'autorisation de l'ensemble des exploitants concernés. Il n'a donc pas été possible de mettre en œuvre l'expérimentation sur plusieurs sites. De même dans le chapitre 2, l'objectif était de trouver des sites présentant l'ensemble du gradient d'humidité présent en Vallée de la Loire, avec des refuges potentiels (haies, bois, prairies xérophiles mais aussi meso-hygrophiles non inondées) avant que la première crue de printemps ne se soit retirée, soit un délai inférieur à une semaine. Là encore, nous n'avons pu trouver qu'un seul site favorable. Nous avons donc choisi d'augmenter considérablement l'effort d'échantillonnage (Lövei, & Magura, 2011) par rapport à ce qui est communément pratiqué dans ce type d'étude, en plaçant jusqu'à 10 répliquats par parcelle (chapitre 1 et 3) ou en augmentant la fréquence d'échantillonnage (chapitre 3). Ainsi, pour ces deux chapitres nous disposions respectivement de 471 et 542 échantillons pour un total de 38670 et 14767 individus, garantissant ainsi la robustesse des résultats.

Structuration des assemblages : échelle locale

Les assemblages d'espèces d'araignées, de carabiques et de plantes des milieux prairiaux sont déterminés par des facteurs locaux et paysagers. Ces facteurs peuvent être biotiques, abiotiques ou en lien avec la gestion des milieux (Hunter, & Price, 1992).

Dans cette étude, nous avons démontré qu'à l'échelle locale, les assemblages d'araignées et de carabiques étaient liés à la hauteur de végétation, à l'épaisseur de litière et à la richesse spécifique en plantes. L'importance de ces facteurs avait déjà été soulignée par de nombreux auteurs. Par exemple, en milieu herbacé, Woodcock et al. (2007) ont démontré que près de 60% des espèces d'araignées de coléoptères répondent à la complexité de l'architecture de la végétation. Uetz (1979) a, lui, démontré que l'abondance de Lycosidae baisse alors que celles de Clubionidae, de Thomisidae et de Gnaphosidae augmentent avec la hauteur et la complexité de la litière. Ce facteur n'est pas cité dans la bibliographie portant sur les carabiques. Cependant, d'après les analyses menées dans le chapitre 1, il s'agirait d'un facteur important pour ce groupe, probablement du fait de la quasi absence de litière dans les parcelles fauchées contrastant avec la parcelle témoin non gérée.

Les liens entre la diversité floristique et celle d'araignées et de carabiques sont moins clairs. En effet, de nombreuses études se basant sur l'hypothèse de la diversité taxonomique ont suggéré un effet positif de cette dernière sur la diversité d'arthropodes y compris sur les araignées (Jeanneret et al., 2003) et les carabiques (Purtauf et al., 2005). Cependant, plusieurs études ont remis en question cette hypothèse pour les araignées (Patrick et al., 2008; Patrick et al., 2012) et les carabiques (Billeter et al., 2007; Gallé et al., 2011). La diversité floristique étant négativement corrélée à la biomasse végétale, nous avons démontré un lien positif entre diversité spécifique et abondance de carabiques et biomasse végétale (Chapitre I). Des liens significatifs mais faibles ont été mis en évidence concernant les araignées, laissant supposer que d'autres facteurs seraient plus prégnants dans la structuration des assemblages d'araignées. Ces résultats suggèrent donc qu'à l'échelle locale un contrôle "bottom-up" de la diversité vient s'ajouter à l'influence des variables citées plus haut.

De plus, nous avons démontré que l'exploitation d'une corrélation entre diversité et abondance d'arthropodes et biomasse végétale par les techniques de télédétection (notamment les indices de végétation) constitue un outil prometteur pour la mise en place de politiques de conservation à large échelle. En effet, le fait de pouvoir prédire la richesse spécifique de certains groupes d'arthropodes peut aider à la définition de hotspots de biodiversité. L'existence de ce lien doit cependant être testée expérimentalement par manipulation de la biomasse végétale. Dans un second temps, puisque nous avons démontré le rôle majeur du paysage dans la structuration de la diversité des arthropodes (Chapitre 6), nous proposons que le lien entre richesse spécifique d'arthropodes et biomasse (approchée par des indices de végétation dérivés d'images satellites) soit testé à plus large échelle et dans des prairies non inondables.

De récentes études suggèrent que si c'est bien la biomasse végétale qui est le facteur explicatif essentiel de ce type de contrôle, ce dernier s'exerce plus fortement encore sur la composition des communautés d'arthropodes (Rzanny et al., 2012). Nos résultats à petite échelle confirment ce point mais faute de données suffisantes (disponibilité d'images satellites de résolutions et de qualités satisfaisantes), nous n'avons pu tester cette hypothèse à large échelle. Il semble donc pertinent de tester non seulement le lien richesse spécifique d'arthropodes/biomasse mais aussi le lien composition des communautés/biomasse.

A ces facteurs, s'ajoutent ceux liés à la spécificité du milieu étudié : les prairies de fauche inondables. Nous avons ainsi démontré dans le chapitre 2 que les araignées et carabiques sont particulièrement bien adaptés aux perturbations stochastiques occasionnées par les crues de printemps puisqu'ils font partie des premiers groupes à recoloniser les prairies. Nous avons cependant constaté que les araignées, et notamment les lycoses, recolonisaient plus rapidement les prairies inondées que les carabiques. Lors de ces inondations de courte durée, les espèces se déplaçant au sol et présentant une forte mobilité semblent donc être plus adaptées à la recolonisation des milieux touchés. Ces résultats ne sont cependant pas généralisables à tous les types de crue. En

effet, il a été démontré que dans les plaines alluviales européennes, les crues estivales peuvent se révéler particulièrement impactantes pour les araignées et carabiques et cela à moyen et long terme (Gerisch et al., 2012).

L'humidité du sol est un facteur largement cité comme influençant les assemblages d'araignées (Entling et al., 2007) et de carabiques (Eyre, 2006). Notre étude confirme ce constat puisque malgré la crue, les parcelles les plus sèches et n'ayant pas été inondées, présentent des assemblages d'espèces très différents de ceux des parcelles humides et ne constituent pas des refuges lors des crues.

La survenue d'une crue au printemps peut constituer un facteur de mortalité important non seulement par destruction directe des individus mais aussi par l'absence de proies qu'elle induit pour des prédateurs ayant déjà subi un jeûne prolongé pendant l'hiver (Petersen, 1999). Les araignées et notamment les Lycosidae, sont reconnues pour être capables d'endurer des périodes de jeûne particulièrement longues, dépassant les 200 jours (Anderson, 1974). Cependant, les capacités de jeûne de carabiques semblent bien plus limitées, se situant en moyenne à 28 jours (Luff, 1994). On peut donc légitimement s'interroger sur le régime alimentaire des individus colonisant les milieux après le retrait de la crue. En effet, la plupart des proies habituelles ne recolonisant le milieux que très lentement, on peut supposer que les *Pardosa* et les *Pterostichus* colonisant le milieu les premiers se nourrissent de biomasse provenant du milieu aquatique comme cela a été démontré chez certains carabiques et araignées ripicoles (Paetzold et al., 2005). Nous proposons donc de mettre en place une étude basée sur les isotopes stables (δ ^{13}C et δ ^{15}N) afin d'étudier le réseau trophique qui se met en place après les crues hivernales et de printemps. Dès le retrait des eaux et jusqu'au mois d'octobre, plusieurs campagnes de prélèvements des différents maillons dominants des chaînes trophiques aquatiques et terrestres pourront être prélevés dans les prairies inondées. Il serait pertinent de réaliser des prélèvements sur les berges de Loire afin de comparer l'importance des échanges aquatiques / terrestres dans des habitats ou plusieurs espèces spécialisées sont déjà connues pour consommer des insectes aquatiques.

De plus, il semble qu'en période de famine, malgré un métabolisme réduit certains arthropodes prédateurs, et notamment les carabiques présentent des mobilités accrues (Frampton, & Cilgi, 1995). Ce constat pourrait expliquer l'activité-densité supérieure des araignées et carabiques après les crues et mériterait donc d'être investigué par capture-recapture de populations soumises ou non à des crues.

Les carabiques présentent un cycle comprenant une phase larvaire endogée. On les divise en deux catégories : les "spring breeders" dont les larves se développent au cours de l'été et les "autumn breeders" dont les larves se développent en hiver. La plupart des espèces rencontrées au cours de cette étude sont des "spring-breeders" qui passent l'hiver à l'état adulte. Dans les secteurs ne présentant que très peu de bocage, la question de la localisation des sites d'hivernage mérite d'être investiguée. Les "autumn breeders" ne sont cependant pas absents des prairies inondables. Ainsi, une population importante de *Carabus monilis* se maintient sur l'Île Saint-Aubin. La question

de la localisation des sites de développement larvaire se pose alors logiquement pour cette espèce brachyptère. Des nasses à émergence pourront être mises en place le long de transects suivant le gradient d'humidité sur différents habitats de la vallée afin d'investiguer ces questions. Cela devra être fait dès le retrait des eaux au début du printemps.

L'impact de la gestion des prairies sur l'entomofaune a lui aussi été largement étudié. Nos résultats corroborent ceux déjà obtenus quant à l'impact négatif de la fauche à court et long terme sur de nombreux groupes d'arthropodes (Rushton et al., 1989; Blake et al., 1996; Rothenbücher, 2004) en prairie. Hormis pour la végétation (Bakker et al., 2002) et les oiseaux (Britschgi et al., 2006), le rôle de la date de fauche a fait l'objet de bien moins d'attention, notamment concernant les arthropodes. Nous avons pu démontrer que l'impact de la date de fauche est relativement faible et se situe essentiellement à court terme, araignées et carabiques n'étant pas affectés de la même façon ni par les mêmes périodes (Chapitre 3). Ainsi, les fauches précoces impactent les araignées en terme de diversité, de densité ainsi qu'en termes fonctionnels (guildes de chasse). A l'inverse les carabiques de grande taille sont affectés par les fauches tardives.
L'impact de la date de fauche sur la diversité floristique est reconnu (Bakker et al., 2002), les fauches précoces favorisant les espèces pérennes compétitives et les fauches tardives les espèces annuelles. On pourrait donc légitimement attendre un impact à long terme de la date de fauche sur les arthropodes puisque nous avons démontré l'existence d'un lien entre diversité floristique et diversité de carabiques. Il est cependant vraisemblable que l'étalement des dates de fauches pratiqué ne soit pas suffisant pour avoir une influence sur la diversité floristique. Il correspond en effet à la période optimale suggérée par Critchley et al. (2007). Il semble donc pertinent de mettre en place un dispositif expérimental permettant de disposer d'un étalement suffisant des dates de fauche afin d'en tester l'impact.
A l'exception de l'étude menée par Humbert et al. (2009) sur les chenilles de papillons, aucune étude n'a été menée quant l'impact du type de fauche (barre de coupe, fauche rotative...) et de la vitesse de fauche. Or, les pratiques agricoles sont en pleine mutation : les barres de coupe sont de plus en plus larges, la fauche rotative se développe et les vitesses ne cessent de croître. Ainsi il paraît pertinent de tester l'effet des différents types de matériel sur les invertébrés.

Structuration des assemblages : large échelle

Dans la seconde partie de cette étude, nous avons cherché à déterminer les facteurs intervenant à large échelle sur les assemblages d'araignées, de carabiques et de plantes. La plus grande emprise spatiale de l'étude permet alors de prendre en compte simultanément des facteurs locaux et paysagers. Quel que soit le groupe étudié, un facteur local ressort systématiquement. L'humidité du sol (liée au régime d'inondation) apparaît ainsi comme un facteur central dans la structuration des assemblages d'espèces. Ce constat confirme les résultats obtenus lors des études à l'échelle

locale et est en accord avec l'abondante bibliographie sur le sujet.

Il est important de noter que dans notre travail (excepté le chapitre 3), l'humidité du sol a été estimée à partir des caractéristiques des communautés végétales présentes. La végétation est en effet un excellent intégrateur des caractéristiques abiotiques du sol (Ter Braak, & Gremmen, 1987; Bouzillé, 2007; Bouzillé, 2014). Les communautés végétales ont été étudiées par une approche phytosociologique selon la méthode de Braun-Blanquet (Braun-Blanquet, 1928). La phytosociologie permet en effet de réaliser une classification des assemblages d'espèces végétales. Dans les grandes vallées fluviales, ces assemblages sont liés en grande partie au régime hydrique (Foucault, 1984) et permettent donc de disposer de classes représentant le gradient d'humidité. Par ailleurs, nous avons aussi utilisé l'indice d'Ellenberg d'humidité (Ellenberg et al., 1992). A partir du profil écologique des espèces végétales le long des gradients écologiques, Ellenberg et al. (1992) ont proposé des indices correspondant aux préférendums des espèces par rapport à sept facteurs écologiques dont l'humidité. Cependant, si les indices d'Ellenberg sont très largement utilisés en écologie, leur pertinence a parfois été remise en cause (Schaffers, & Sýkora, 2000). Il semblerait donc important de vérifier leur pertinence en plaine alluviale. Pour cela des mesures d'humidité du sol pourraient être réalisées à intervalles réguliers, pour chaque grand type d'habitat et sur plusieurs sites de la Vallée de la Loire au cours de plusieurs saisons végétatives complètes.
Selon Rzanny et al. (2012) la composition spécifique des communautés de plantes est de loin le meilleur prédicteur de la composition spécifique des groupes fonctionnels d'arthropodes dont les prédateurs. Nos résultats, à travers l'utilisation d'une approche phytosociologique pour la détermination des classes/indices d'humidité, confirment donc ce constat et plaident pour une prise en compte plus systématique des assemblages d'espèces végétales dans les études portant sur les arthropodes y compris prédateurs.

Le faible impact de la date de fauche sur les araignées et carabiques, mis en évidence dans le chapitre 1, est quand à lui, encore minimisé par les résultats obtenus à large échelle. En effet, il semble que l'humidité du sol, et donc le régime d'inondation, soit un facteur bien plus important pour expliquer la densité et la diversité des assemblages d'arthropodes en prairie humide.
A l'inverse, la gestion présente une importance qui peut se révéler considérable concernant la végétation. En effet, une baisse de l'intensité de gestion (ici absence de pâturage de regain) peut favoriser les espèces compétitives (Ryel et al., 1996) et entraîner une baisse de la diversité végétale et de la biomasse (Amiaud et al., 1996; Bouzillé et al., 2010). En revanche, les modulations de gestion préconisées dans le cadre des MAE portant sur la date de fauche et la quantité d'intrants ne semblent pas avoir d'impact sur les assemblages de plantes. Tout comme pour les arthropodes il semble que le facteur "humidité" soit plus important que la date de fauche. Concernant les intrants, il est probable que ce soit les apports alluviaux de biomasse qui soient le véritable facteur déterminant.

Les mesures agri-environnementales portant aussi sur le pâturage, nous proposons qu'une démarche similaire soit suivie sur les prairies menées en pâture afin de vérifier si l'interdiction des traitements anti-parasitaires, la limitation des chargements et l'encadrement des dates de mise en pâture ont un impact sur les richesses en arthropodes. Le sujet est d'autant plus intéressant que deux pratiques s'opposent en Vallée de la Loire. En effet, alors que dans l'estuaire les pâtures sont en majorité situées en bord de Loire et donc soumises très régulièrement à des inondations liées aux grandes marées, les pâtures situées en amont sont généralement en retrait des berges de Loire et donc exposées uniquement aux crues hivernales.
Par ailleurs, la prégnance de l'humidité sur les assemblages d'araignées et de carabiques, couplée à nos résultats sur la cartographie des associations phytosociologiques nous invite à tester dans l'avenir la prédiction des assemblages à partir de cartographies d'humidité générées après classification supervisée d'images satellites. Cette approche pourrait de plus être couplée à l'utilisation d'indices de végétation tels que l'EVI 2. Ces tests pourraient ne pas se limiter aux araignées et carabiques. En effet, les orthoptères sont des phytophages dont la densité et la diversité varient fortement avec la biomasse végétale et l'humidité (Wingerden et al., 1992). On peut donc logiquement supposer que des modèles croisant indices d'humidité et de végétation à partir d'images satellites permettent de mieux appréhender leur répartition.

Le rôle du paysage (sa nature et son organisation) dans la structuration des assemblages d'arthropodes et de plantes a été mis en évidence à de nombreuses reprises. Cependant, son importance fait encore l'objet de débats concernant la diversité d'araignées. Ainsi, la contribution du paysage à la structuration des communautés d'araignées semblerait dépendre du milieu étudié (Jeanneret et al., 2003) mais aussi de la composante de diversité (α, β ou γ) étudiée (Hendrickx et al., 2007). Ici, nous avons démontré que dans les prairies de fauche inondables les diversités α d'araignées et de carabiques sont surtout liées à des facteurs paysagers. A l'inverse, la diversité α de plantes est liée à des facteurs locaux.
Les carabiques sont généralement considérés comme particulièrement sensibles à l'organisation du paysage et notamment à la connectivité (Burel, 1989; Duflot et al., 2014). Ce facteur, s'il est important pour expliquer la diversité des carabiques reste moins important que la nature du paysage (ici la nature du sol).
Les résultats concernant la diversité β sont sensiblement les mêmes pour les araignées et la végétation. En revanche, de façon surprenante, la diversité β des carabiques est principalement liée à des facteurs locaux puis dans une moindre mesure à la connectivité du milieu liée au bocage. L'importance de cette dernière n'est cependant pas négligeable et vient confirmer les résultats obtenus dans le chapitre 2. Nous avons en effet démontré le rôle de refuge et donc, par la suite, de source lors de la recolonisation des prairies, joué par le bocage pour les espèces recolonisant par déplacement au sol (lycoses chez les araignées et gros carabiques). Contrairement aux carabiques, les analyses menées dans le chapitre 6 suggèrent un faible rôle de la connectivité dans la

structuration des communautés d'araignées. Cependant, il convient de noter que les techniques d'échantillonnage utilisées lors de ces deux études étaient différentes, l'une étant plus adaptée à la capture des lycoses que l'autre.

La part relative des facteurs locaux et paysagers dans la structuration des communautés d'arthropodes en termes de diversité spécifique pourrait être différente de celle concernant la composition spécifique des assemblages (Rzanny et al., 2012). Nous proposons donc par la suite de mener des analyses complémentaires sur le même jeu de données afin de mieux cerner le rôle relatif des facteurs locaux et paysagers dans la structuration des assemblages spécifiques.

Conséquences pour la gestion de la biodiversité des prairies humides

La gestion des milieux prairiaux est actuellement essentiellement axée sur la préservation des espèces végétales et des oiseaux à travers les mesures agri-environnementales (MAE). Ces deux groupes ne représentent cependant qu'une infime partie de la diversité biologique (Cardoso et al., 2011). Ainsi, malgré le fait qu'ils représentent près de 80% des espèces décrites, les arthropodes sont généralement peu pris en compte par les politiques de protection de la biodiversité à l'exception de quelques groupes bien connus de part leur aspect esthétique (lépidoptères, odonates) ou pour les services écologiques qu'ils rendent (coléoptères saproxiliques et plus récemment pollinisateurs). Les araignées et coléoptères carabiques ont très récemment fait l'objet d'un intérêt particulier en lien avec leur potentiel rôle d'auxiliaire des cultures (Symondson et al., 2002). Ces deux groupes représentent de plus une large part de la biomasse animale des prairies (Cardoso et al., 2011) et présentent une forte diversité spécifique. Ainsi 267, espèces d'arthropodes (143 espèces d'araignées et 124 espèces de carabiques) ont été inventoriées lors de cette étude pour 249 espèces de plantes. Les arthropodes méritent donc particulièrement d'être pris en compte dans les politiques de conservation et cela passe évidemment par une meilleure connaissance de leur écologie et de leur répartition.

Dans le chapitre 1, nous avons mis en évidence une forte corrélation négative entre biomasse et diversité végétale ainsi qu'un lien positif entre biomasse végétale et diversité de carabiques. Ainsi, alors que les efforts de conservation visent systématiquement à augmenter la diversité floristique des milieux, on constate qu'en Vallée de la Loire, les parcelles les moins diversifiées du point de vue végétal sont celles qui présentent la plus grande diversité carabidologique.
Sur le secteur d'étude, les MAE portent essentiellement sur le retard de date de fauche supposé permettre aux jeunes oiseaux prairiaux d'être volants au moment des fauches (Brereton et al., 2007) et sur la limitation de la fertilisation permettant de limiter la perte de diversité floristique

(Critchley et al., 2004).
Bien que non corrélée à l'humidité de la parcelle, les dates de fauche les plus précoces sont généralement prises sur les parcelles les plus sèches. Ces parcelles, qui comportent la diversité d'araignées la plus forte ont donc tendance à être fauchées à la période la plus néfaste pour ce groupe. A l'inverse, nous avons démontré que les carabiques de grosse taille, considérés comme les plus en danger (Kotze et al., 2011), sont plus impactés par les fauches tardives. Concernant le troisième groupe étudié, selon Critchley et al. (2007), la diversité végétale des prairies européennes est, elle, maximisée pour des fauches ayant lieu entre mi-juin et mi-juillet (medium à tardives). Il ne semble donc pas exister de date de fauche idéale permettant de maximiser la biodiversité dans son ensemble.
Les MAE portent en second lieu sur la limitation de la fertilisation. L'objectif est alors de maximiser la diversité végétale. La fertilisation azotée a un effet positif sur la diversité d'araignées (jusqu'à un certain seuil) et sur la diversité floristique pour des seuils supérieurs à ceux recommandés par les MAE. Ainsi, la limitation de la fertilisation azotée ne semble pas pertinente dans les prairies inondables.

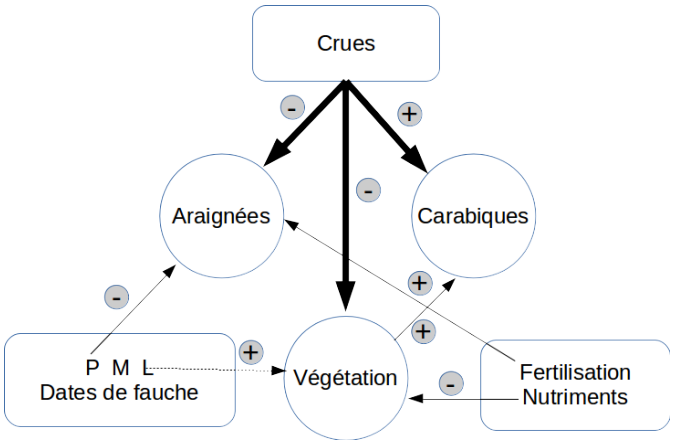

Figure 6.7 – Schéma de l'impact des mesures de gestion sur la diversité d'araignées et de carabiques. La largeur des flèches indique l'importance du facteur. Les flèches en pointillés correspondent à des influences attendues mais non démontrées. P: précoce; M: moyenne; L: tardive.

Au vu de ces résultats, il nous semble important de recommander une approche non "parcelle-centrée" lors de la détermination des mesures de gestion. En effet, puisqu'aucune date de fauche n'est optimale pour l'ensemble des groupes, il convient de spatialiser les mesures afin de favoriser l'hétérogénéité des pratiques.
Par ailleurs, les parcelles les plus sèches ne pouvant faire l'objet de retard de fauche sans perte importante de valeur fourragère, il semble pertinent de proposer la mise en place de bandes ou patchs non fauchés qui serviront de refuge à la faune (Cizek et al., 2012). L'efficacité de ces bandes a été mise en évidence sur divers groupes (oiseaux: Broyer, 2003, carabiques: Kromp, 1999,

araignées: Nentwig, 1988). La plupart des études sur le rôle des bandes enherbées portant sur les grandes cultures ou sur des prairies non soumises aux crues, nous proposons donc la mise en place de tests à moyen terme (l'âge jouant sur leur efficacité Ranjha, & Irmler, 2013) sur l'impact des bandes enherbées dans les prairies inondables.
Enfin, nous avons pu démontrer qu'à large échelle ces mesures de gestion influencent peu la diversité et l'abondance des arthropodes et de la végétation en comparaison de l'humidité du sol (figure 6.7). Bien que la Loire soit souvent citée comme le dernier fleuve sauvage de France, son fonctionnement est loin d'être naturel puisque de nombreuses levées (sortes de digues latérales) la corsètent et que des barrages sont présents sur son cours et sur ces principaux affluents. Sur le secteur d'étude, le fonctionnement hydrologique du fleuve a été fortement modifié par les extractions de sable et le creusement d'un bassin de marée entraînant une baisse de la ligne d'eau du fleuve et un assèchement des milieux adjacents au fleuve. Un programme de remontée de la ligne d'eau est en cours de préparation. S'il devait atteindre ses objectifs, l'ensemble des communautés animales et végétales des milieux bordant le fleuve serait impacté. Il est donc impératif que de tels projets intègrent un volet recherche sur les impacts des changements opérés sur la faune et la flore.

Dans le chapitre 2, nous avons pu mettre en évidence l'importance du bocage dans la recolonisation des prairies après une crue de printemps. On peut supposer que son rôle puisse se révéler encore plus important lors d'une crue estivale. Ces résultats plaident bien-sûr pour le maintien d'un réseau bocager important. Ce rôle est en outre souligné par l'importance de la fermeture du milieu par le bocage pour la diversité des carabiques (Chapitre 6). Cependant, il a récemment été démontré que cette fermeture était négative pour les populations d'oiseaux prairiaux (Besnard et al., 2014). Il convient donc de maintenir le bocage sur les secteurs déjà riches en haies et d'empêcher la plantation sur les dernières grandes prairies accueillant des oiseaux prairiaux en Vallée de la Loire.
Nous avons cependant démontré que les diversités d'araignées et de carabiques sont essentiellement liées au type de sol et que celle des plantes est liée aux nutriments et à l'humidité. Les mesures visant à améliorer les pratiques de gestion n'ont donc que peu d'efficacité, si ce n'est pour les oiseaux prairiaux et cela uniquement hors des années avec crues de printemps (Besnard et al., 2014). Dans leur état actuel, elles doivent donc être vues comme un moyen efficace de maintenir les prairies humides naturelles plutôt que comme un moyen d'améliorer la biodiversité.

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Annexes

Listes des espèces d'invertébrés capturées

Table 1 – Liste des espèces d'araignées capturées et effectifs.

Famille	Espèce	Effectifs
Agelenidae	*Agelena sp.*	1
Araneidae	*Araneidae sp.*	49
	Hypsosinga albovittata (Westring, 1851)	10
	Hypsosinga pygmaea (Sundevall, 1831)	6
	Hypsosinga sp.	1
	Larinioides cornutus (Clerck, 1758)	1
	Mangora acalypha (Walckenaer, 1802)	39
Clubionidae	*Clubiona pseudoneglecta* (Wunderlich, 1994)	14
	Clubiona sp.	14
Corinnidae	*Phrurolithus festivus* (C.L. Koch, 1835)	26
Dictynidae	*Argenna patula* (Simon, 1874)	8
	Argenna sp.	2
	Argenna subnigra (O. P.-Cambridge, 1861)	33
Gnaphosidae	*Civizelotes civicus* (Simon, 1878)	42
	Drassodes lapidosus (Walckenaer, 1802)	5
	Drassyllus lutetianus (L. Koch, 1866)	570
	Drassyllus praeficus (L. Koch, 1866)	11
	Drassyllus pusillus (C.L. Koch, 1833)	55
	Haplodrassus dalmatensis (L. Koch, 1866)	43
	Haplodrassus minor (O. P.-Cambridge, 1879)	2
	Haplodrassus signifer (C.L. Koch, 1839)	107
	Haplodrassus sp.	9
	Micaria albovittata (Lucas, 1846)	1
	Micaria pulicaria (Sundevall, 1831)	5
	Micaria sp.	1
	sp.	4
	Trachyzelotes pedestris (C.L. Koch, 1837)	7
	Zelotes latreillei (Simon, 1878)	9
	Zelotes longipes (L. Koch, 1866)	1
	Zelotes sp.	37
	Zelotes subterraneus (C.L. Koch, 1833)	1
Hahniidae	*Hahnia nava* (Blackwall, 1841)	9
Linyphiidae	*Allomengea vidua* (L. Koch, 1879)	111
	Araeoncus humilis (Blackwall, 1841)	3
	Bathyphantes gracilis (Blackwall, 1841)	130
	Bathyphantes parvulus (Westring, 1851)	13
	Centromerus capucinus (Simon, 1884)	1
	Ceratinella brevipes (Westring, 1851)	3
	Ceratinella brevis (Wider, 1834)	5

	Diplocephalus graecus (O. P.-Cambridge, 1872)	34
	Diplocephalus latifrons (O. P.-Cambridge, 1863)	1
	Diplostyla concolor (Wider, 1834)	11
	Erigone atra (Blackwall, 1833)	90
	Erigone dentipalpis (Wider, 1834)	240
	Erigone sp.	2
	Gnathonarium dentatum (Wider, 1834)	7
	Gongylidiellum murcidum (Simon, 1884)	2
	Gongylidiellum vivum (O. P.-Cambridge, 1875)	1
	Maso gallicus (Simon, 1894)	14
	Meioneta affinis (Kulczynski, 1898)	10
	Meioneta innotabilis (O. P.-Cambridge, 1863)	2
	Meioneta mollis (O. P.-Cambridge, 1871)	110
	Meioneta rurestris (C.L. Koch, 1836)	306
	Meioneta saxatilis (Blackwall, 1844)	6
	Meioneta simplicitarsis (Simon, 1884)	19
	Mermessus trilobatus (Emerton, 1882)	9
	Metopobactrus prominulus (O. P.-Cambridge, 1872)	2
	Micrargus subaequalis (Westring, 1851)	4
	Microlinyphia pusilla (Sundevall, 1829)	11
	Oedothorax agrestis (Blackwall, 1853)	1
	Oedothorax fuscus (Blackwall, 1834)	250
	Oedothorax retusus (Westring, 1851)	6
	Palliduphantes ericaeus (Blackwall, 1853)	1
	Palliduphantes insignis (O. P.-Cambridge, 1913)	1
	Palliduphantes pallidus (O. P.-Cambridge, 1871)	3
	Panamomops sulcifrons (Wider, 1834)	9
	Parapelecopsis nemoralis (Blackwall, 1841)	2
	Pelecopsis mengei (Simon, 1884)	1277
	Pelecopsis parallela (Wider, 1834)	96
	Pelecopsis sp.	26
	Pocadicnemis juncea (Locket & Millidge, 1953)	3
	Porrhomma microphthalmum (O. P.-Cambridge, 1871)	3
	Porrhomma pygmaeum (Blackwall, 1834)	1
	Prinerigone vagans (Savigny in Audouin, 1825)	62
	Savignia frontata (Blackwall, 1833)	2
	Silometopus ambiguus (O. P.-Cambridge, 1905)	8
	Silometopus elegans (O. P.-Cambridge, 1872)	24
	Sintula retroversus (O. P.-Cambridge, 1875)	1
	sp.	3928
	Tenuiphantes flavipes (Blackwall, 1854)	1
	Tenuiphantes tenuis (Blackwall, 1852)	967
	Tenuiphantes zimmermanni (Bertkau, 1890)	3
	Tiso vagans (Blackwall, 1834)	9
	Trichoncus saxicola (O. P.-Cambridge, 1861)	22
	Troxochrus scabriculus (Westring, 1851)	2
	Walckenaeria atrotibialis (O. P.-Cambridge, 1878)	1
Lycosidae	*Alopecosa accentuata* (Latreille, 1817)	1
	Alopecosa barbipes (Sundevall, 1832)	2
	Alopecosa cuneata (Clerck, 1758)	467
	Alopecosa pulverulenta (Clerck, 1758)	24
	Arctosa fulvolineata (Lucas, 1846)	7

	Arctosa leopardus (Sundevall, 1832)	36
	Aulonia albimana (Walckenaer, 1805)	1
	Pardosa agrestis (Westring, 1861)	325
	Pardosa agricola (Thorell, 1856)	18
	Pardosa amentata (Clerck, 1758)	7
	Pardosa hortensis (Thorell, 1872)	1
	Pardosa nigriceps (Thorell, 1856)	3
	Pardosa palustris (Linnaeus, 1758)	884
	Pardosa prativaga (L. Koch, 1870)	10791
	Pardosa proxima (C.L. Koch, 1848)	1988
	Pardosa pullata (Clerck, 1758)	135
	Pardosa sp.	1021
	Pardosa vittata (Keyserling, 1863)	62
	Pirata latitans (Blackwall, 1841)	4
	Pirata piraticus (Clerck, 1758)	12
	Pirata sp.	4
	sp.	7227
	Trochosa hispanica (Simon, 1870)	339
	Trochosa robusta (Simon, 1876)	9
	Trochosa spinipalpis (F.O. P.-Cambridge, 1895)	25
	Trochosa terricola Thorell, 1856	49
	Trochosa sp.	24
	Xerolycosa miniata (C.L. Koch, 1834)	2
	Xerolycosa nemoralis (Westring, 1861)	1
Mimetidae	*Ero aphana* (Walckenaer, 1802)	1
	Ero furcata (Villers, 1789)	1
Miturgidae	*Cheiracanthium pennyi* (O.P.-Cambridge, 1873)	2
Nesticidae	*Nesticus cellulanus* (Clerck, 1758)	1
Philodromidae	*Thanatus sp.*	2
	Thanatus striatus C.L. Koch, 1845	74
	Tibellus oblongus (Walckenaer, 1802)	5
Pisauridae	*Pisaura mirabilis* (Clerck, 1758)	11
Salticidae	*Ballus chalybeius* (Walckenaer, 1802)	1
	Euophrys frontalis (Walckenaer, 1802)	3
	Euophrys herbigrada (Simon, 1871)	1
	Evarcha arcuata (Clerck, 1758)	4
	Heliophanus flavipes (Hahn, 1831)	3
	Sibianor aurocinctus (Ohlert, 1865)	1
	sp.	6
	Talavera aequipes (O. P.-Cambridge, 1871)	3
	Talavera aperta (Miller, 1971)	5
Tetragnathidae	*Pachygnatha clercki* (Sundevall, 1823)	135
	Pachygnatha degeeri (Sundevall, 1829)	97
	Pachygnatha sp.	8
	Tetragnatha extensa (Linnaeus, 1758)	7
	Tetragnatha sp.	6
Theridiidae	*Asagena phalerata* (Panzer, 1801)	12
	Crustulina sticta (O. P.-Cambridge, 1861)	1
	Enoplognatha mordax (Thorell, 1875)	303
	Enoplognatha ovata (Clerck, 1758)	2
	Enoplognatha sp.	6
	Enoplognatha thoracica (Hahn, 1833)	3

	Neottiura bimaculata (Linnaeus, 1767)	14
	Neottiura suaveolens (Simon, 1879)	29
	Phylloneta impressa (Koch, 1881)	4
	sp.	66
Thomisidae	*Ozyptila praticola* (C.L. Koch, 1837)	2
	Ozyptila rauda (Simon, 1875)	10
	Ozyptila simplex (O. P.-Cambridge, 1862)	1481
	Ozyptila trux (Blackwall, 1846)	16
	Ozyptila sp.	308
	sp.	141
	Xysticus acerbus (Thorell, 1872)	1
	Xysticus cristatus (Clerck, 1758)	1
	Xysticus erraticus (Blackwall, 1834)	20
	Xysticus kochi (Thorell, 1872)	195
	Xysticus lanio (C.L. Koch, 1835)	1
	Xysticus luctuosus (Blackwall, 1836)	26
	Xysticus sp.	9
Zoridae	*Zora parallela* (Simon, 1878)	8
	Zora spinimana (Sundevall, 1833)	5
-	*sp.*	26
Total		35 558

TABLE 2 – Liste des espèces de carabiques capturées et effectifs.

Tribu	Espèce	Effectif
Bembidiini	*Bembidion assimile* (Gyllenhal, 1810)	14
	Metallina lampros (Herbst, 1784)	23
	Metallina properans (Stephens, 1828)	6
	Notaphus dentellus (Thunberg, 1787)	125
	Notiophilus biguttatus (Fabricius, 1779)	40
	Notiophilus substriatus (C.R. Waterhouse, 1833)	1
	Philochthus biguttatus (Fabricius, 1779)	179
	Philochthus iricolor (Bedel, 1879)	74
	Phyla tethys (Netolitzky, 1926)	1
	Trepanes gilvipes (Sturm, 1825)	1
	Trepanes octomaculatus (Goeze, 1777)	3
Brachinini	*Brachinus bodemeyeri* (Apfelbeck, 1904)	1
	Brachinus elegans (Chaudoir, 1842)	16
	Brachinus psophia (Audinet-Serville, 1821)	10
Carabini	*Carabus granulatus* (Linnaeus, 1758)	706
	Carabus monilis (Fabricius, 1792)	127
	Carabus sp.	2
Chlaeniini	*Chlaeniellus nigricornis* (Fabricius, 1787)	18
	Chlaeniellus tristis (Schaller, 1783)	1
	Chlaenius chrysocephalus (P. Rossi, 1790)	2
Clivinini	*Clivina fossor* (Linnaeus, 1758)	879
Dryptini	*Drypta dentata* (P. Rossi, 1790)	1
Dyschiriini	*Dyschiriodes globosus* (Herbst, 1783)	4
	Dyschirius angustatus (Ahrens, 1830)	1
Elaphridae	*Elaphrus riparius* (Linnaeus, 1758)	3
Harpalini	*Acupalpus dubius* (Schilsky, 1888)	2
	Acupalpus exiguus (Dejean, 1829)	493
	Anisodactylus binotatus (Fabricius, 1787)	109
	Anisodactylus poeciloides (Stephens, 1828)	10
	Anthracus consputus (Duftschmid, 1812)	9
	Carterus fulvipes (Latreille, 1817)	3
	Cryptophonus litigiosus (Dejean, 1829)	1
	Cryptophonus melancholicus (Dejean, 1829)	2
	Cryptophonus tenebrosus (Dejean, 1829)	3
	Diachromus germanus (Linnaeus, 1758)	165
	Gynandromorphus etruscus (Quensel in Schönherr, 1806)	1
	Harpalus affinis (Schrank, 1781)	1103
	Harpalus anxius (Duftschmid, 1812)	120
	Harpalus atratus (Latreille, 1804)	2
	Harpalus attenuatus (Stephens, 1828)	81
	Harpalus cupreus (Dejean, 1829)	342
	Harpalus dimidiatus (P. Rossi, 1790)	574
	Harpalus dispar (Dejean, 1829)	1
	Harpalus distinguendus (Duftschmid, 1812)	13
	Harpalus luteicornis (Duftschmid, 1812)	86
	Harpalus melancholicus (Dejean, 1829)	1
	Harpalus modestus (Dejean, 1829)	10
	Harpalus picipennis (Duftschmid, 1812)	1
	Harpalus politus (Dejean, 1829)	11

	Harpalus serripes (Quensel in Schönherr, 1806)	162
	Harpalus servus (Duftschmid, 1812)	2
	Harpalus smaragdinus (Duftschmid, 1812)	1
	Microlestes minutulus (Goeze, 1777)	230
	Ophonus ardosiacus (Lutshnik, 1922)	20
	Ophonus opacus (Dejean, 1829)	4
	Ophonus sabulicola (Panzer, 1796)	198
	Parophonus mendax (P. Rossi, 1790)	1
	Pseudoophonus griseus (Panzer, 1796)	196
	Pseudoophonus rufipes (De Geer, 1774)	3606
	Stenolophus mixtus (Herbst, 1784)	19
	Stomis pumicatus (Panzer, 1796)	5
	Syntomus obscuroguttatus (Duftschmid, 1812)	428
	Synuchus vivalis (Illiger, 1798)	2
Licinini	*Badister (Baudia) collaris* (Motschulsky, 1844)	2
	Badister (Trimorphus) sodalis (Duftschmid, 1812)	1
Loricerini	*Loricera pilicornis* (Fabricius, 1775)	6
Nebriini	*Nebria brevicollis* (Fabricius, 1792)	14
Oodini	*Oodes gracilis* (A. Villa & G.B. Villa, 1833)	1
	Oodes helopioides (Fabricius, 1792)	17
Panagaeini	*Panagaeus cruxmajor* (Linnaeus, 1758)	1
Platynini	*Agonum fuliginosum* (Panzer, 1809)	5
	Agonum marginatum (Linnaeus, 1758)	1
	Agonum nigrum (Dejean, 1828)	11
	Anchomenus dorsalis (Pontoppidan, 1763)	7
	Platynus livens (Gyllenhal, 1810)	1
Pogonini	*Pogonus chalceus* (Marsham, 1802)	2
Pterostichini	*Poecilus cupreus* (Linnaeus, 1758)	4100
	Poecilus kugelanni (Panzer, 1797)	6
	Poecilus versicolor (Sturm, 1824)	7
	Pterostichus anthracinus (Illiger, 1798)	76
	Pterostichus cursor (Dejean, 1828)	4
	Pterostichus diligens (Sturz, 1824)	3
	Pterostichus gracilis (Dejean, 1828)	5
	Pterostichus macer (Marsham, 1802)	2
	Pterostichus melanarius (Illiger, 1798)	584
	Pterostichus minor (Gyllenhal, 1827)	2
	Pterostichus niger (Schaller, 1783)	4
	Pterostichus oblongopunctatus (Fabricius, 1787)	4
	Pterostichus quadrifoveolatus (Letzner, 1852)	16
	Pterostichus vernalis (Panzer, 1796)	24
Sphodrini	*Calathus ambiguus* (Paykull, 1790)	1
	Calathus fuscipes (Dejean, 1831)	299
	Calathus melanocephalus (Linnaeus, 1758)	1
Trechini	*Epaphius secalis* (Paykull, 1790)	13
	Trechoblemus micros (Herbst, 1784)	1
	Trechus quadristriatus (Schrank, 1781)	1
Zabrini	*Amara aenea* (De Geer, 1774)	45
	Amara anthobia (A. Villa & G.B. Villa, 1833)	1
	Amara bifrons (Gyllenhal, 1810)	5
	Amara communis (Panzer, 1797)	33
	Amara concinna (Zimmermann, 1832)	29

	Amara curta (Dejean, 1828)	1
	Amara equestris (Duftschmid, 1812)	2
	Amara erythrocnema (Dejean, 1828)	120
	Amara eurynota (Panzer, 1797)	7
	Amara familiaris (Duftschmid, 1812)	20
	Amara floralis (Gaubil, 1844)	2
	Amara fulvipes (Audinet-Serville, 1821)	40
	Amara fusca (Dejean, 1828)	1
	Amara kulti (Fassati, 1947)	1
	Amara littorea (C.G. Thomson, 1857)	1
	Amara lunicollis (Schiödte, 1837)	15
	Amara majuscula (Chaudoir, 1850)	1
	Amara montivaga (Sturm, 1825)	9
	Amara morio (Ménétriés, 1832)	1
	Amara plebeja (Gyllenhal, 1810)	81
	Amara rufipes (Dejean, 1828)	27
	Amara similata (Gyllenhal, 1810)	3
	Amara strenua (Zimmermann, 1832)	159
	Amara tibialis (Paykull, 1798)	1
	Amara tricuspidata (Dejean, 1831)	6
	Zabrus tenebrioides (Goeze, 1777)	3
Zuphiini	*Polistichus connexus* (Geoffroy in Fourcroy, 1785)	1
Total		16 092

TABLE 3 – Liste des familles, hors araignées et carabiques capturées et effectifs.

Classe	Ordre	Famille	Effectif
Arachnida	**Acaridida**	-	191
	Ixodida	-	60
	Mesostigmata	Gamasida	43
	Opiliones	Sironidae	2
	Trombidiformes	-	186
Chilopoda	**Lithobiomorpha**	-	23
Clitellata	**Haplotaxida**	Lumbricidae	15
Gasteropoda	**Stylommatophora**	Arionidae	378
		Helicidae	10
Insecta	**Coleoptera**	Anthicidae	65
		Byrrhidae	44
		Cantharidae	7
		Chrysomelidae	5
		Coccinellidae	51
		Curculionidae	407
		Helophoridae	55
		Histeridae	249
		Nitidulidae	15
		Scarabaeidae	11
		Staphylinidae	270
	Diptera	Calliphordae	1
		Chloropidae	39
		Lauxaniidae	2
		Muscidae	45
		Scatopsidae	35
		Sciaridae	52
		Sphaeroceridae	8
		Tephritidae	7
		Tipulidae	3
	Hemiptera	Alydidae	2
		Aphididae	153
		Cicadellidae	27
		Cydnidae	26
		Miridae	16

		Pentatomidae	12
		Tingidae	16
	Hymenoptera	Apidae	31
		Cynipidae	5
		Diapriidae	1
		Evanioidea	11
		Formicinae	1430
		Ichneumonoidae	34
		Myrmicinae	873
		Vespidae	7
	Lepidoptera	Polydesma	92
	Orthoptera	Acrididae	222
		Tetrigidae	10
Malacostraca	**Isopoda**	Asellidae	88
		Oniscidae	37
Total			5 372

TABLE 4 – Liste des espèces de plantes inventoriées et pourcentage de présence dans les relevés

Famille	Espèce	%
Alismataceae	Alisma lanceolatum With., 1796	0,94
	Alisma plantago-aquatica L., 1753	2,04
	Atriplex prostrata Boucher ex DC., 1805	0,16
	Allium oleraceum L., 1753	0,63
	Allium sp.	2,2
	Allium vineale L., 1753	4,4
Apiaceae	Chaerophyllum temulum L., 1753	0,16
	Daucus carota L., 1753	0,63
	Eryngium campestre L., 1753	4,24
	Eryngium maritimum L., 1753	0,16
	Oenanthe fistulosa L., 1753	24,65
	Oenanthe pimpinelloides L., 1753	1,1
	Oenanthe silaifolia M.Bieb., 1819	45,37
	Silaum silaus (L.) Schinz & Thell., 1915	5,02
	Sium latifolium L., 1753	0,47
Asparagaceae	Asparagus officinalis L., 1753	0,16
	Muscari comosum (L.) Mill., 1768	0,63
Asteraceae	Achillea ptarmica L., 1753	15,7
	Bellis perennis L., 1753	9,26
	Centaurea jacea L., 1753	6,28
	Centaurea jacea subsp. grandiflora (Gaudin) Schübler & G.Martens, 1834	14,6
	Centaurea sp.	0,16
	Cirsium arvense (L.) Scop., 1772	14,13
	Cirsium vulgare (Savi) Ten., 1838	0,16
	Crepis biennis L., 1753	0,16
	Crepis capillaris (L.) Wallr., 1840	4,24
	Crepis sp.	0,16
	Crepis vesicaria L., 1753	0,16
	Gnaphalium sp.	0,16
	Gnaphalium uliginosum L., 1753	0,16
	Helminthotheca echioides (L.) Holub, 1973	0,47
	Helminthotheca sp.	0,16
	Hypochaeris radicata L., 1753	9,11
	Inula britannica L., 1753	7,69
	Inula sp.	0,31
	Jacobaea aquatica (Hill) P.Gaertn., B.Mey. & Scherb., 1801	48,19
	Jacobaea vulgaris Gaertn., 1791	2,2
	Leontodon hispidus L., 1753	1,1
	Leontodon sp.	0,16
	Leucanthemum vulgare Lam., 1779	2,98
	Scorzonera humilis L., 1753	0,16
	Scorzoneroides autumnalis (L.) Moench, 1794	15,54
	Scorzoneroides autumnalis subsp. borealis (Ball) Greuter, 2006	0,16
	Solidago virgaurea L., 1753	1,1
	Sonchus asper (L.) Hill, 1769	2,35
	Symphyotrichum lanceolatum (Willd.) G.L.Nesom, 1995	0,31
	Taraxacum officinale F.H.Wigg., 1780	17,74
	Taraxacum sp.	5,34
	Tragopogon pratensis L., 1753	5,34

	Achillea millefolium L., 1753	0,63
	Bidens frondosa L., 1753	0,47
Boraginaceae	Myosotis laxa Lehm., 1818	4,55
	Myosotis scorpioides L., 1753	3,3
	Myosotis secunda A.Murray, 1836	2,67
	Myosotis sp.	1,41
	Symphytum officinale L., 1753	13,34
	Myosotis discolor Pers., 1797	0,63
Brassicaceae	Brassica nigra (L.) W.D.J.Koch, 1833	0,31
	Capsella bursa-pastoris (L.) Medik., 1792	0,94
	Cardamine amara L., 1753	0,31
	Cardamine parviflora L., 1759	0,47
	Cardamine pratensis L., 1753	7,85
	Raphanus raphanistrum L., 1753	4,24
	Rorippa amphibia (L.) Besser, 1821	0,31
	Rorippa sylvestris (L.) Besser, 1821	1,41
	Sisymbrium officinale (L.) Scop., 1772	0,31
	Lepidium heterophyllum Benth., 1826	0,16
Butomaceae	Butomus umbellatus L., 1753	0,47
Campanulaceae	Campanula persicifolia L., 1753	0,47
	Campanula rapunculus L., 1753	0,31
Caprifoliaceae	Valeriana officinalis L., 1753	0,16
Caryophyllaceae	Arenaria serpyllifolia L., 1753	0,47
	Cerastium dubium (Bastard) Guépin, 1838	2,83
	Cerastium glomeratum Thuill., 1799	6,91
	Cerastium sp.	0,16
	Herniaria glabra L., 1753	0,16
	Lychnis flos-cuculi L., 1753	12,56
	Silene nutans L., 1753	0,16
	Stellaria graminea L., 1753	1,57
	Stellaria media (L.) Vill., 1789	0,16
	Stellaria sp.	0,31
Celastraceae	Euonymus europaeus L., 1753	0,16
Convolvulaceae	Calystegia sepium (L.) R.Br., 1810	5,49
	Convolvulus arvensis L., 1753	21,66
Cyperaceae	Carex acuta L., 1753	4,55
	Carex cuprina (Sandor ex Heuff.) Nendtv. ex A.Kern., 1863	9,11
	Carex disticha Huds., 1762	3,45
	Carex divisa Huds., 1762	4,71
	Carex elata All., 1785	0,31
	Carex flacca Schreb., 1771	0,16
	Carex hirta L., 1753	3,45
	Carex nigra (L.) Reichard, 1778	2,2
	Carex ovalis Gooden., 1794	1,73
	Carex pilulifera L., 1753	0,63
	Carex praecox Schreb., 1771	0,16
	Carex riparia Curtis, 1783	0,78
	Carex sp.	5,97
	Carex spicata Huds., 1762	3,14
	Carex strigosa Huds., 1778	0,16
	Carex vesicaria L., 1753	0,16
	Carex vulpina L., 1753	3,14

	Cyperus longus L., 1753	1,88
	"Eleocharis palustris (L.) Roem. & Schult., 1817"	12,24
	Eleocharis uniglumis (Link) Schult., 1824	10,83
	Schoenoplectus lacustris (L.) Palla, 1888	0,16
	Schoenoplectus tabernaemontani (C.C.Gmel.) Palla, 1888	0,16
	Bolboschoenus maritimus (L.) Palla, 1905	0,47
Equisetaceae	Equisetum arvense L., 1753	1,57
	Equisetum pratense Ehrh., 1784	0,63
	Equisetum palustre L., 1753	0,16
	Euphorbia esula L., 1753	2,67
	Euphorbia sp.	0,31
Fabaceae	Genista tinctoria L., 1753	0,31
	Lathyrus nissolia L., 1753	0,16
	Lathyrus palustris L., 1753	1,26
	Lathyrus pratensis L., 1753	15,23
	Lotus corniculatus L., 1753	26,69
	Lotus glaber Mill., 1768	1,73
	Lotus pedunculatus Cav., 1793	0,31
	Lotus sp.	0,63
	Medicago arabica (L.) Huds., 1762	2,83
	Medicago littoralis Rohde ex Loisel., 1810	0,16
	Medicago lupulina L., 1753	0,16
	Medicago polymorpha L., 1753	0,31
	Medicago sativa L., 1753	1,41
	Trifolium arvense L., 1753	0,31
	Trifolium campestre Schreb., 1804	1,41
	Trifolium dubium Sibth., 1794	10,68
	Trifolium fragiferum L., 1753	11,46
	Trifolium hybridum L., 1753	0,31
	Trifolium incarnatum L., 1753	0,47
	Trifolium michelianum Savi, 1798	4,4
	Trifolium pratense L., 1753	10,52
	Trifolium repens L., 1753	15,23
	Trifolium resupinatum L., 1753	1,1
	Trifolium sp.	0,31
	Trifolium squamosum L., 1759	6,75
	Trifolium subterraneum L., 1753	0,16
	Trisetum flavescens (L.) P.Beauv., 1812	1,57
	Vicia cracca L., 1753	29,98
	Vicia disperma DC., 1813	0,47
	Vicia faba L., 1753	0,16
	Vicia hirsuta (L.) Gray, 1821	3,92
	Vicia parviflora Cav., 1801	0,16
	Vicia sativa L., 1753	12,09
	Quercus robur L., 1753	0,47
Geraniaceae	Geranium dissectum L., 1755	19,47
	Geranium molle L., 1753	0,31
	Erodium cicutarium (L.) L'Hér., 1789	0,94
Hypericaceae	Hypericum perforatum L., 1753	0,63
Iridaceae	Iris pseudacorus L., 1753	3,77
Juncaceae	Juncus acutiflorus Ehrh. ex Hoffm., 1791	0,94
	Juncus articulatus L., 1753	0,16

	Juncus compressus Jacq., 1762	0,16
	Juncus conglomeratus L., 1753	0,16
	Juncus effusus L., 1753	3,14
	Juncus gerardi Loisel., 1809	2,2
	Juncus inflexus L., 1753	1,26
	Juncus sp.	0,31
	Luzula campestris (L.) DC., 1805	0,47
Lamiaceae	Lamium purpureum L., 1753	0,31
	Mentha aquatica L., 1753	3,77
	Mentha arvensis L., 1753	0,94
	Mentha pulegium L., 1753	1,26
	Prunella vulgaris L., 1753	0,63
	Scutellaria galericulata L., 1753	0,16
	Scutellaria hastifolia L., 1753	0,63
	Stachys palustris L., 1753	9,26
Liliaceae	Fritillaria meleagris L., 1753	8,32
Linaceae	Linum usitatissimum subsp. angustifolium (Huds.) Thell., 1912	0,31
Lythraceae	Lythrum salicaria L., 1753	1,26
Malvaceae	Althaea officinalis L., 1753	9,11
	Malva moschata L., 1753	0,16
Oleaceae	Fraxinus angustifolia Vahl, 1804	0,63
	Fraxinus excelsior L., 1753	1,26
Onagraceae	Epilobium parviflorum Schreb., 1771	0,16
	Epilobium sp.	0,16
Orchidaceae	Anacamptis laxiflora (Lam.) R.M.Bateman, Pridgeon & M.W.Chase, 1997	0,31
	Neotinea ustulata (L.) R.M.Bateman, Pridgeon & M.W.Chase, 1997	0,16
Orobanchaceae	Orobanche caryophyllacea Sm., 1798	0,47
	Orobanche sp.	0,16
	Rhinanthus alectorolophus (Scop.) Pollich, 1777	0,16
Plantaginaceae	Gratiola officinalis L., 1753	5,34
	Plantago lanceolata L., 1753	40,97
	Plantago major L., 1753	0,94
	Plantago media L., 1753	0,31
	Plantago sp.	0,16
	Veronica arvensis L., 1753	2,83
	Veronica anagallis-aquatica L., 1753	1,1
	Veronica catenata Pennell, 1921	0,31
	Veronica serpyllifolia L., 1753	0,16
	Veronica sp.	0,16
Plumbaginaceae	Armeria arenaria (Pers.) Schult., 1820	0,31
Poaceae	Agrostis canina L., 1753	0,47
	Agrostis capillaris L., 1753	1,57
	Agrostis sp.	0,31
	Agrostis stolonifera L., 1753	42,23
	Alopecurus bulbosus Gouan, 1762	8,48
	Alopecurus geniculatus L., 1753	4,4
	Alopecurus pratensis L., 1753	53,06
	Alopecurus sp.	0,16
	Anisantha diandra (Roth) Tutin ex Tzvelev, 1963	0,16
	Anisantha sterilis (L.) Nevski, 1934	0,78
	Anthoxanthum odoratum L., 1753	19,94
	Arrhenatherum elatius s. elatius	18,52

	Arrhenatherum elatius subsp. bulbosum (Willd.) Schübler & G.Martens, 1834	1,1
	Briza media L., 1753	0,31
	Bromus commutatus Schrad., 1806	4,71
	Bromus hordeaceus L., 1753	11,93
	Bromus racemosus L., 1762	21,51
	Calamagrostis epigejos (L.) Roth, 1788	0,47
	Cynodon dactylon (L.) Pers., 1805	1,88
	Cynosurus cristatus L., 1753	11,62
	Dactylis glomerata L., 1753	8,01
	Elymus caninus (L.) L., 1755	2,51
	Elytrigia repens (L.) Desv. ex Nevski, 1934	52,12
	Festuca ovina L., 1753	1,57
	Festuca rubra L., 1753	0,63
	Festuca sp.	1,57
	Gaudinia fragilis (L.) P.Beauv., 1812	5,34
	Glyceria fluitans (L.) R.Br., 1810	4,08
	Glyceria maxima (Hartm.) Holmb., 1919	5,18
	Holcus lanatus L., 1753	16,8
	Hordeum murinum L., 1753	0,47
	Hordeum secalinum Schreb., 1771	27,16
	Hordeum sp.	0,31
	Leersia oryzoides (L.) Sw., 1788	0,16
	Lolium multiflorum Lam., 1779	0,63
	Lolium perenne L., 1753	51,81
	Micropyrum tenellum (L.) Link, 1844	0,47
	Phalaris arundinacea L., 1753	26,84
	Phleum pratense L., 1753	6,91
	Phragmites australis (Cav.) Trin. ex Steud., 1840	3,3
	Poa annua L., 1753	0,31
	Poa pratensis L., 1753	8,63
	Poa trivialis L., 1753	60,6
	Schedonorus arundinaceus (Schreb.) Dumort., 1824	2,83
	Schedonorus pratensis (Huds.) P.Beauv., 1812	0,78
	Vulpia bromoides (L.) Gray, 1821	5,18
	Vulpia myuros (L.) C.C.Gmel., 1805	0,31
Polygonaceae	Persicaria amphibia (L.) Gray, 1821	17,27
	Rumex acetosa L., 1753	25,75
	Rumex acetosella L., 1753	1,57
	Rumex conglomeratus Murray, 1770	9,11
	Rumex crispus L., 1753	25,27
	Rumex sanguineus L., 1753	0,47
	Rumex thyrsiflorus Fingerh., 1829	4,08
Primulaceae	Lysimachia nummularia L., 1753	3,3
	Lysimachia vulgaris L., 1753	10,99
Ranunculaceae	Ranunculus acris L., 1753	35,16
	Ranunculus aquatilis L., 1753	0,31
	Ranunculus bulbosus L., 1753	3,45
	Ranunculus flammula L., 1753	5,81
	Ranunculus ophioglossifolius Vill., 1789	0,31
	Ranunculus repens L., 1753	39,72
	Ranunculus sardous Crantz, 1763	9,73
	Ranunculus sceleratus L., 1753	0,16

	Thalictrum flavum L., 1753	11,46
Rosaceae	Argentina anserina (L.) Rydb., 1899	3,3
	Filipendula ulmaria (L.) Maxim., 1879	0,16
	Potentilla recta L., 1753	0,16
	Potentilla reptans L., 1753	20,41
	Rubus fruticosus L., 1753	0,31
	Rubus sp.	0,16
	Sanguisorba officinalis L., 1753	0,31
Rubiaceae	Galium aparine L., 1753	0,63
	Galium debile Desv., 1818	1,73
	Galium mollugo L., 1753	0,47
	Galium palustre L., 1753	25,59
	Galium sp.	0,16
	Galium verum L., 1753	15,7
Typhaceae	Sparganium erectum L., 1753	0,94
Urticaceae	Urtica dioica L., 1753	1,73

Denis Lafage

Curriculum vitae

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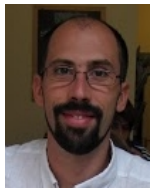

PhD Student

Main skills

Scientific Research	— Study design and management — Data analysis and interpretation of results — Writing / reviewing of scientific articles — Research funding (up to 200 000 €project) — Project management (budget, logistics, etc.) — Analytical and deductive reasoning	Statistics Computer	— Data management: Access — Scientific: R, Fragstat ... — GIS: QGIS, GRASS, ArcGis, MapInfo — Miscellaneous: Linux, LaTeX, ...
Relational	— Team and independent work — Coordination and management of a small team and students — Meeting organization and conduct — Good writing capabilities — Adaptability and reliability	Nature	— Entomology (spiders, carabid beetles, dragonflies) — Ornithology (waterbirds) — Mammalogy (certified bat capturer, acoustic)

Education

2003–2004 **Msc**, *Universty Via Domitia*, Perpignan.
Environment and sustainable development

2002–2003 **MSc**, *Muséum National d'Histoire Naturelle*, Paris.
Environment, Technics and Folks

2001–2002 **Bsc**, *University of Rennes 1*, Rennes.
Population and Organisms Biology

Experience

Vocational

2011-2014 **PhD Student**, *EA 7316 Biodiversité Gestion des Territoires*, University of Rennes 1.

- Drivers of arthropod and plant communties in flooded grasslands
- Arthropods ecology
- Use of remote sensing technologies in biodiversity conservation

2008–... **In charge of biodiversty assessment**, *CORELA*, Nantes.

Detailed achievements:

- Fonctionnality of grasslands in the Loire Valley
- Inventory, monitoring and conservation of bat roosts in the Loire Valley
- Mapping landcover and hedgerow network of the Loire Valley

2004–2008 **In charge of scientific monitoring**, *Domaine de la Palissade*, Salin de Giraud.

- Fauna monitoring: waterbirds, amphibians, mammals
- Flora monitoring: grasslands, invasive species
- Impact of mosquito control by Bti on waterbirds
- Site managment
- Nature guide

Scientific projects

2012–... **OBLA: Biodiversity observatory of the Loire Valley**.

- Terrestrial arthropods group coordinator

2011-2012 **CARHAB: Cartographie des habitats français**.

2011 **Vulnerability of Loire ecosystems to global warming**.

- Member of the managment committee

Miscellaneous

Various handling jobs.

International meetings

As invited speaker

- Vegetation mapping in Europe. Saint Mandé (France), 17th - 19th October , 2013

As speaker

- Open landcapes 2013. Hildesheim (Germany). 29th September - 3rd October 2013
- 19th International congress of arachnology. Taïwan, 23rd - 28th June 2013
- European Vegetation Survey 19th Workshop. Pécs (Hungary), 29th April - 2nd May 2010

Poster

- European Vegetation Survey. 21st Workshop Vienna (Austria), 24th - 27th May 2012

National meetings as speaker

- National congress of arachnology. Fouras (France). 5th October 2012

Referee

- Diversity and Distribution

Publications

D. Lafage, A. Bonis, L. Menanteau, and J-B. Bouzillé. Using landscape metrics on satellite imagery to assess the conservation status of grassland plant communities. *Applied Vegetation Science*, Major revision, 2014.

D. Lafage, C. Papin, J. Secondi, A. Canard, and J. Pétillon. Short term recolonisation by arthropod after a spring flood, with a focus on spiders and carabids. *Ecohydrology*, Submited, 2014.

D. Lafage and J. Pétillon. Impact of cutting date on carabids and spiders in a wet meadow. *Agriculture, Ecosystems & Environment*, 185:1–8, 2014.

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P. Laffaille, C. Briand, D. Fatin, D. Lafage, and E. Lasne. Point sampling the abundance of European eel (Anguilla anguilla) in freshwater areas. *Archiv für Hydrobiologie*, 162(1):91–98, 2005.

M. Varet, F. Burel, D. Lafage, and J. Pétillon. Age-dependent colonisation of urban habitats : a diachronic approach using carabid beetles and spiders. *Animal Biology*, 63:257–269, 2013.

Languages

English **Independant user** *B2*

Spanish **Independant user** *B1*

Interests

Sports Swimming, diving (level 2), hiking

Arts Photography

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